RESEARCH ARTICLE

First records and new information on the associations of echinoderms with other phyla in the rocky reefs of northern Chocó, Colombian Pacific

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Abstract

Rocky reefs of the northern Colombian Pacific (Chocó) are diverse ecosystems that are poorly studied. Echinoderms are one of the principal groups in these ecosystems with associations to different species, including benthic organisms in which they live and other species that use them as hosts. These relationships include fishes, sponges, seaweeds, cnidarians, polychaetes, bryozoans, crustaceans, mollusks, and other echinoderms. For this area, 22 associations were registered, including commensalism, epibionts and parasitism. This work constitutes the first report for the associations of *Eucidaris thouarsii* with *Suberites* aff. *ficus*, *E. thouarsii* with *Ophiothela mirabilis*, and *Holothuria* (*Thymiosicia*) *impatiens* with *Encheliophis vermicularis.* Associations of *Pentaceraster cumingi* with *Zenopontonia soror*, and *Ophionereis annulata* with *Malmgreniella* cf. *variegata* are new records for Colombia. This work also expands the range of hosts previously described for *Ophiothela mirabilis* and expands the distribution of the association between *Diadema mexicanum* and *Echineulima* cf. *robusta*.

Keywords

Commensalism, epibionts, parasitism, Asteroidea, Echinoidea, Holothuroidea, Ophiuroidea, Riscales

Introduction

Echinoderms are distributed in all coastal environments from tidal pools to rocky and coral reefs, in which they share space and refuge areas with members of their own phylum and other taxa (Sotelo-Casas and Rodríguez-Troncoso 2014). Due to this closeness, different types of interactions have been developed; within these associations are found the ones in which echinoderms depends on other organisms such as sponges and octocorals for protection against predators and for easy access to food (Henkel and Pawlik 2005, Marin et al. 2005). Others in which echinoderms interact with other organisms and the substrate, for example species that depend on the fixing cavities constructed by sea urchins such as *Echinometra lucunter lucunter* (Linnaeus, 1758) (Schoppe 1991).The cavities of this sea urchin, from the Caribbean Sea, are used by the brittle star *Ophiothrix synoecina* (Schoppe, 1996) which is obligated symbiont of *E. lucunter lucunter* (Schoppe 1996; Schoppe and Werding 1996). Finally, the mutualism occurring between different species of detritivorous sea cucumbers that share their inhabiting spaces and adopt different schedules for feeding and positions allowing other species to take advantage of the food (Rupert and Barnes 1996).

Relationships occur in all echinoderm classes; for example, the starfishes are frequently inhabited by symbionts of various taxonomic groups such as polychaetes, copepods, and mollusks (Jangoux 1990, Antokhina et al. 2012), with some species that are obligate symbionts (i.e., *Hololepidella millari*, *Doridicola echinasteris*) (Antokhina and Britayev 2012). For sea cucumbers, interactions with at least nine phyla have been described including diatoms, protozoans, flat worms (i.e., Xenacoelomorphos), polychaetes, mollusks, crustaceans, fish, and even other echinoderms (Jangoux 1990, Eeckhaut et al. 2004, Purcell et al. 2016). Related to sea urchins, different types of relationships have also been established, including commensalism with animals as the crab *Stenorhynchus debilis* (Smith, 1871) and a fish of the genus *Apogon* for which the sea urchin spines served as a refuge (Sotelo-Casas and Rodríguez-Troncoso 2014), and sponges that use the spines of sea urchins as an attachment substrate (Hétérier and De Ridder 2004, Aguirre et al. 2011). Although studies on crinoids are very limited, the association and dependence of many of the myxostomid species (Annelida) with this group has been recorded; approximately 100 of the 150 species of myxostomid currently described live above or within crinoids during their adult stage (Summers and Rouse 2014). For brittle stars, interactions with different kind of organisms have been reported, by having different adaptations in color and the brittle stars *Ophionereis* behavior to simulate the host, this is the case of the polynoid *Harmothroe lunulata*, *Ophionereis reticulata* and *O. annulata* (Millott 1953, Granja-Fernández et al. 2013, Gómez-Maduro and Díaz-Díaz 2017). Finally, many associations with benthic organisms such as sponges have been described in relation to ophiuroids (Bejarano et al. 2004, Marin et al. 2005), in some cases they depend specifically on other organisms for their development (Pardo et al. 1988).

The most studied marine groups related to their interactions with echinoderms are Mollusca and Crustacea. Mainly bivalve and gastropod relationships have been recognized (Caullery 1952), with more than 30 species of prosobranchs recorded as parasites of echinoderms (Caullery 1952), especially echinoids (Hyman 1955). It has also been found that most groups of crustaceans have some type of association with echinoderms, for example cirripedes are considered endo- and ectosymbionts of species such as *Dendrogaster* spp. (Caullery 1952), isopods have both obligate and non-specific relationships with all the five classes of echinoderms, and shrimps include species that are obligated commensals of some echinoderms (Ross 1983).

Relationships between echinoderms and different types of organisms have been widely registered throughout the world, but these are poorly studied and understood in Colombian waters and in the entire Tropical Eastern Pacific. To this end, relationships of the echinoderms with other phyla were recorded during a project developed to characterize the biodiversity of the rocky reefs of Chocó Norte in Colombia.

Materials and methods

Individuals were collected during two expeditions carried out on April and October 2016 in the northern area of the Colombian Pacific, Chocó Department (Figure 1), between Cabo Corrientes in the south (5°29'N, 77°32'W) and Cabo Marzo in the north (6°49'N, 77°41'W). Those expeditions were performed to increase the knowledge in terms of diversity and distribution of the marine biodiversity of the rocky reefs of the area. In the Tropical Eastern Pacific, rocky reefs (called "Riscales" and "Morros" in Chocó), represent habitats for many invertebrate species, including corals, sea fans, and fishes, making them important and productive ecosystems for artisanal fishing (Rubio and Angulo 2003). Some of the rocky reefs are submerged, rising above the level of low tide or forming small permanently emerged islets (Díaz et al. 2016).

Samplings were made using scuba diving, and a direct and random collection of echinoderms was made by sweeping each station looking for all potential habitats in different areas of the rocky reef, at all depths starting at 25 m and finishing at 5 m, the top of the submerged reefs. All field information was recorded for each individual collected, including depth and habitat. The collected echinoderms were relaxed using magnesium chloride dissolved with sea water ($MgCl_2.6H_2O$) and fixed in 96% ethanol. Specimens were morphologically reviewed, photographed, and identified using stereoscope and microscopes. In order to correctly identify sea cucumbers, body wall ossicles were examined.

During the study, all the associated organisms were photographed in field, separated from the echinoderm when possible, and identified by expert taxonomists of each of the groups. The photographs taken in field were reviewed in order to complement the information of the associations, especially those that included octocorals to confirm the distribution range of the associations. Posterior samplings in the same
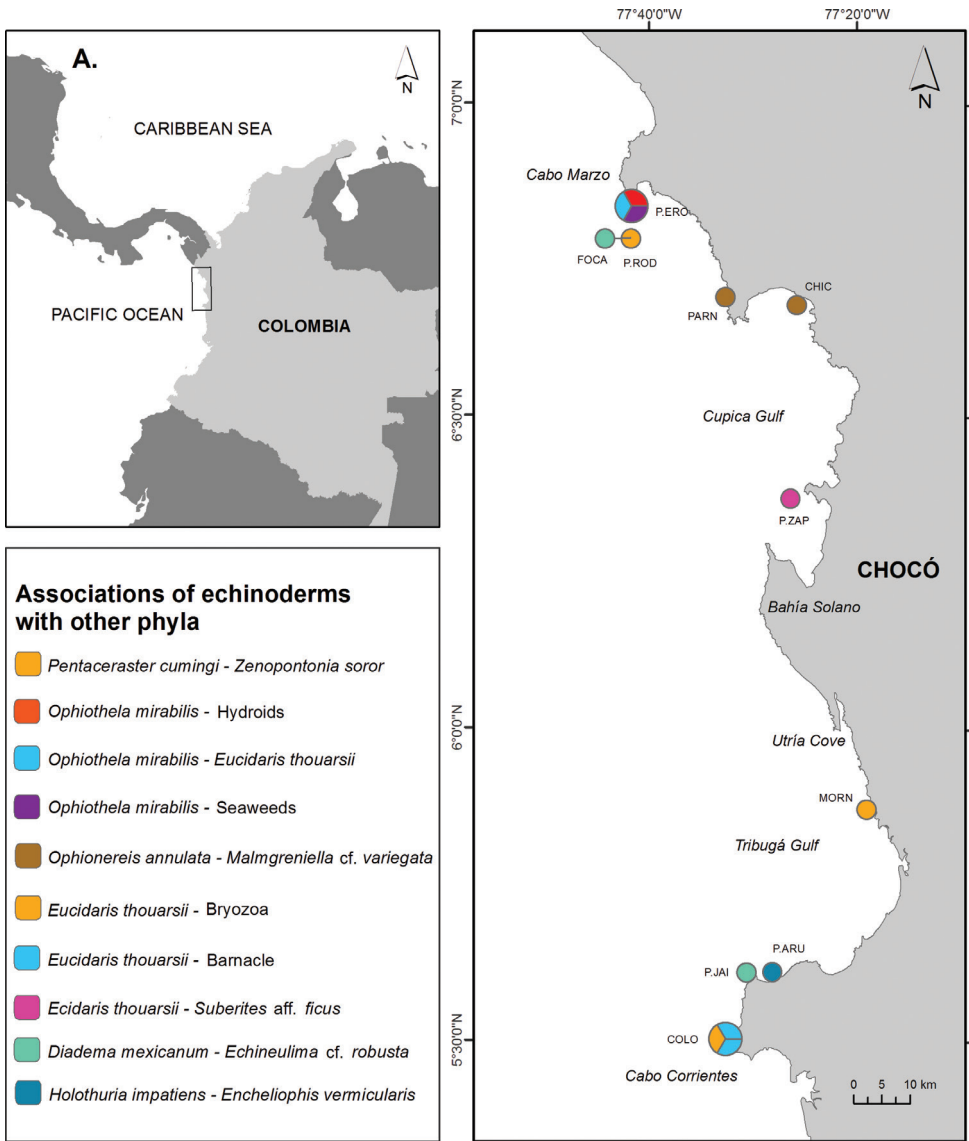
Figure 1. A Locations along northern Colombian Pacific (Chocó) where associations of echinoderms with other phyla were collected. Locations names from north to south P.ERO: Piedra de Eroito, FOCA: la foca, P.ROD: Piedra de Rodrigo, MINA: La mina, PARN: Parguera norte, VIUD: la Viuda, CHIC: Chicocora, P.ZAP: Piedra Zapata, P.NOR: Punta norte, MORN: Morromico norte, JURU: Jurubidá, P.ORI: Punta Orión, P.BON: Piedra bonita, PARS: Parguera sur, P.ARU: Punta Arusí, P.JAI: Piedra de Jairo, ROÑO: Roñosa, AMGR: Amargal, COLO: Coló. The line between FOCA and FARO represents the proximity between both stations.

area, carried out during 2017 and 2018 and focused mainly on octocoral biodiversity of the same locations, allowed us to expand the information on these relationships and are included in this work too.
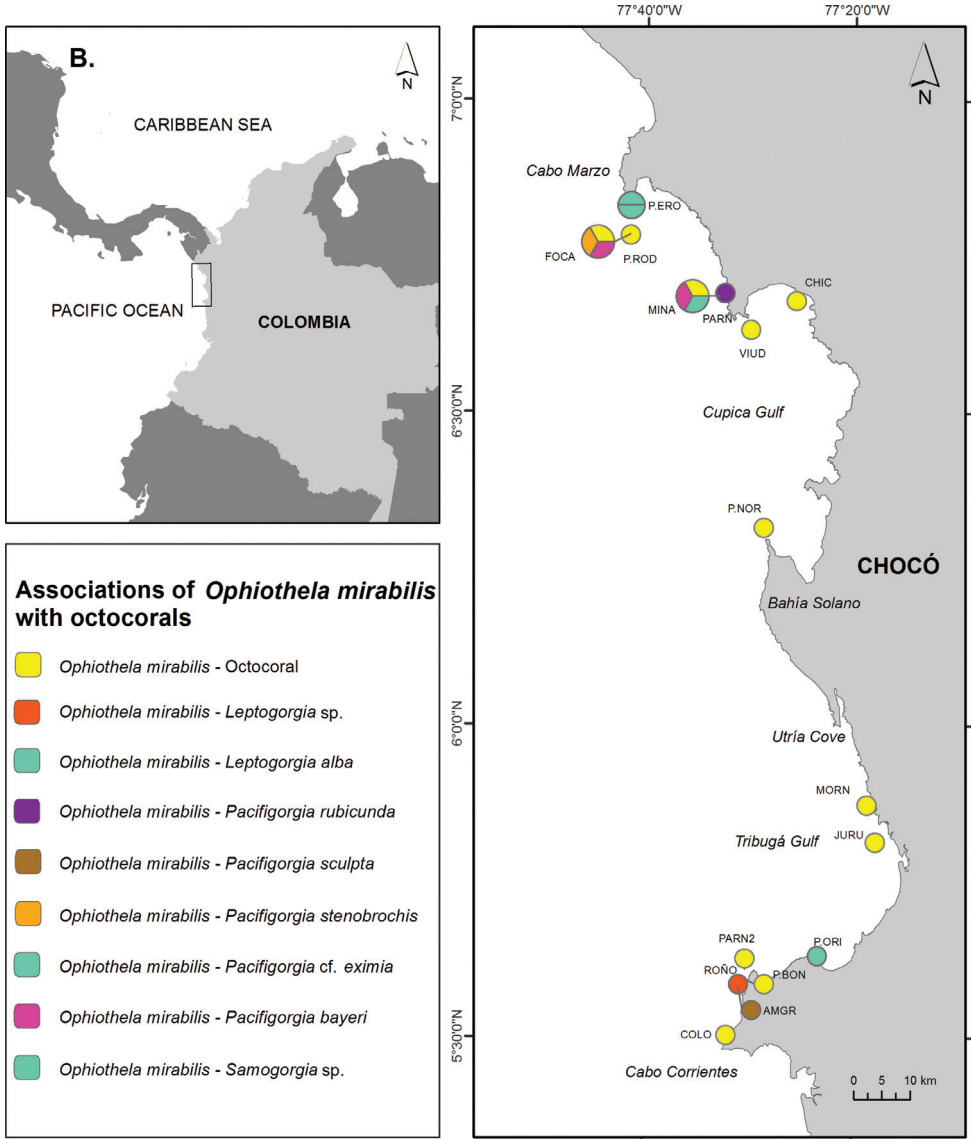
Figure 1. Continued: **B** Locations were associations between *O. mirabilis* and octocorals were registered. Locations names from north to south P.ERO: Piedra de Eroito, FOCA: la foca, P.ROD: Piedra de Rodrigo, MINA: La mina, PARN: Parguera norte, VIUD: la Viuda, CHIC: Chicocora, P.ZAP: Piedra Zapata, P.NOR: Punta norte, MORN: Morromico norte, JURU: Jurubidá, P.ORI: Punta Orión, P.BON: Piedra bonita, PARS: Parguera sur, P.ARU: Punta Arusí, P.JAI: Piedra de Jairo, ROÑO: Roñosa, AMGR: Amargal, COLO: Coló. The lines among several locations represent the proximity between them.

All the collected material was deposited in the biological collections from the Museo de Historia Natural Marina de Colombia (**MHNMC**) – Makuriwa of INVEMAR.

Results and discussion

A total of 22 relationships were registered between echinoderms and other organisms in the rocky reefs of the northern Chocó in the Colombian Pacific. These relationships include fish, sponges, cnidarians, polychaetes, bryozoans, crustaceans, and mollusks (Table 1). All the individuals were identified to the lowest possible taxonomic level, excepting some specimens that were registered only in photographs.

Pentaceraster cumingi (Gray, 1840) – *Zenopontonia soror* (Nobili, 1904)
Figure 2

Material: one specimen of *Pentaceraster cumingi* (INV EQU4283) was collected with two shrimps (*Zenopontonia soror*) located in the oral part (Figure 2). Shrimps were orange, the same color that the ambulacral feet of the sea star. This relationship was recorded in Piedra de Rodrigo (P.ROD) (Figure 1).

Table 1. Relationships between echinoderms and other marine groups found in the rocky reefs of northern Chocó, Colombian Pacific. Key for the relationships C: Commensalism, E: Epibiont, P: Parasitism. Key for Micro-habitats 1: Exposed in the Rocky reef, 2: Exposed in other living organisms, 3: Under rocks in contact with sand, 4: Partially exposed in the Rocky reef, 5: Partially exposed between rocks.

| Echinoderm	Other organisms	Relationship	Micro-habitat	Depth (m)	Figure
Pentaceraster cumingi	*Zenopontonia soror*	C	1	19	Figure 2
Ophiothela mirabilis	*Eucidaris thouarsii*	E	2	7	Figure 3C
	Leptogorgia alba	C	2	3–19	Figure 3A
	Leptogorgia sp.	C	2	3–19	
	Pacifigorgia adamsi	C	2	7–19	Figure 3H
	Pacifigorgia bayeri	C	2	5–19	Figure 3C
	Pacifigorgia eximia	C	2	7–19	Figure 3E
	Pacifigorgia irene	C	2	7–19	Figure 3B
	Pacifigorgia rubicunda	C	2	15	Figure 3F
	Pacifigorgia stenobrochis	C	2	7–19	
	Pacifigorgia sculpta	C	2	25	
	Samogorgia sp.	C	2	7–19	
	Muricea squarrosa	C	2	7	
	Cnidarians	E	2	5	
	Seaweeds	E	2		
Ophionereis annulata	*Malmgreniella* cf. *variegata*	C	3	15	Figure 4
Eucidaris thouarsii	Bryozoans	E	4		Figure 5
	Suberites aff. *ficus*	E	5	9	Figure 5B
	Barnacles	E	4		Figure 5
	Ophiothela mirabilis	E	4		Figure 5C
Diadema mexicanum	*Echineulima* cf. *robusta*	P	4	19	Figure 6
Holothuria impatiens	*Encheliophis vermicularis*	P	3	7	Figure 7
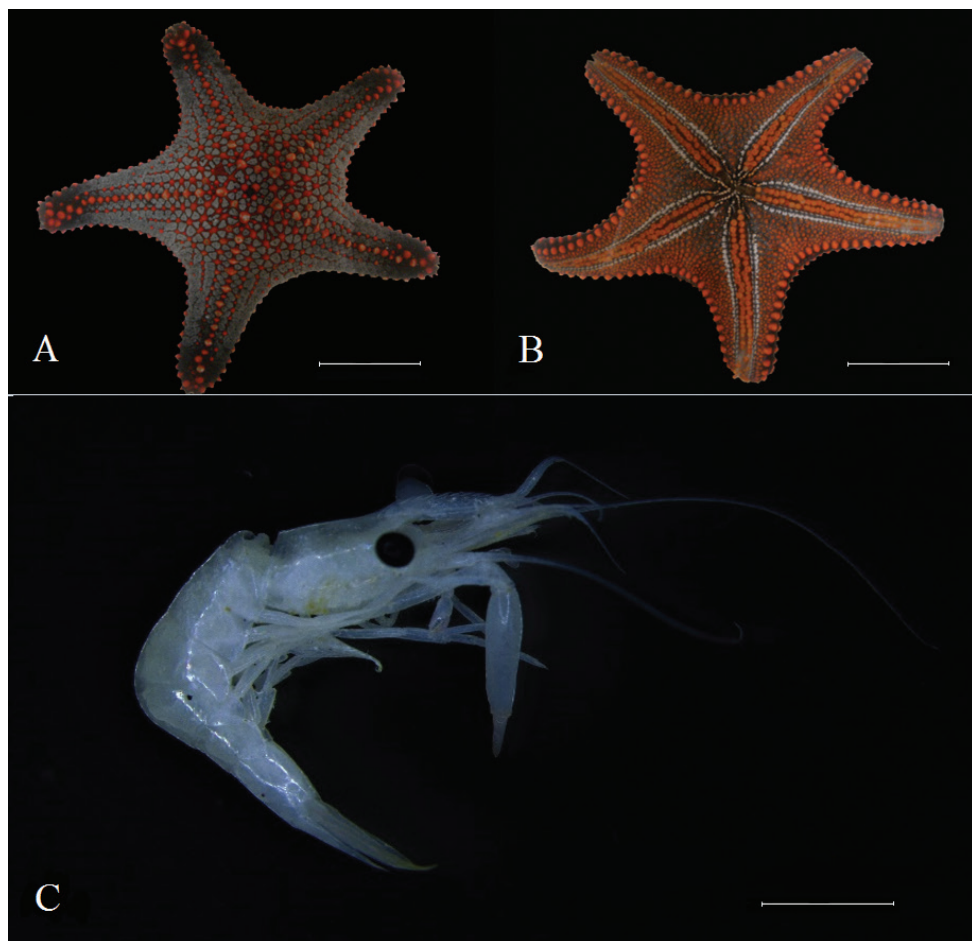
Figure 2. A *Pentaceraster cumingi* aboral view **B** *P. cumingi* oral view **C** *Zenopontonia soror*. The shrimp lost the color after fixing in 96% ethanol. Scale bars: 100 mm (**A, B**), 2 mm (**C**).

Starfish are frequently inhabited by several symbiotic animals (Jangoux 1990). Within the genus *Pentaceraster* the association with *Zenopontonia soror* has been commonly reported world-wide. This commensal shrimp belongs to the family Palaemonidae and is known for being a specialized and obligate symbiont of starfishes (Antokhina and Britayev 2012). *Zenopontonia soror* was initially described in the Red Sea (Nobili 1904), but Edmonson (1935) and Gordon (1939) reported its association with some species of asteroids of the Indo-Pacific, and finally Bruce (1976) reported it in Australia associated with *Plectaster decanus* (Müller & Troschel, 1843) and in Pacific of Panama with *Pentaceraster cumingi* (as *Oreaster occidentalis*) (Bruce 1976), both sea stars being common in reefs. *Zenopontonia soror* is currently reported associated with 21 asteroids species, including five species of the genus *Pentaceraster* (Antokhina and Britayev 2012). This is the first report of the association between *Zenopontonia soror* and *Pentaceraster cumingi* for the Colombian Pacific.

Ophiothela mirabilis Verrill, 1867 and several symbiosis associations
Figure 3

Material: *Ophiothela mirabilis* was registered on different hosts: *Eucidaris thouarsii* (INV EQU4218) (Figure 5C), cnidarians (Figure 3I), seaweeds, and octocorals: *Leptogorgia alba* (Duchassaing y Michelotti, 1864) (INV EQU4251) (Figure 3A, D), *Leptogorgia* sp., *Pacifigorgia rubicunda* Breedy y Guzman, 2003 (Figure 3B), *Pacifigorgia eximia* (Verrill, 1868) (Figure 3C), *Pacifigorgia irene* Bayer, 1951 (Figure 3E), *Pacifigorgia stenobrochis* (Valenciennes, 1846) (Figure 3F), *Pacifigorgia sculpta* Breedy & Guzman, 2004 (Figure 3G), *Pacifigorgia bayeri* Breedy, 2001 (Figure 3H), *Pacifigorgia adamsi* (Verrill, 1868), *Samogorgia* sp. and *Muricea squarrosa* Verrill, 1869. One cnidarian morphotype, possibly a hydrozoan, and the seaweeds could not be identified because they were not collected. *Ophiothela mirabilis'* relationship with octocorals was observed in 16 stations during April (2016) including Chicocora (CHIC), la Foca (FOCA), la Mina (MINA), Parguera (PARN), Piedra de Eroito (P.ERO), Punta norte (P.NOR), Piedra de Rodrigo (P.ROD), la viuda (VIUD), Coló (COLO), Morromico norte (MORN), Jurubidá (JURU), la Roñosa (ROÑO), Amargal (AMGR), Parguera norte (PARN2), Piedra bonita (P.BON) and Punta Orión (P.ORI). In October (2016) no octocoral was registered with this brittle star; however, the relationship was observed in subsequent samplings developed in October 2017 (not included on this work) and 2018.

Brittle stars are usually associated with organisms such as sponges, cnidarians, sea urchins, and even algae which provide shelter and a place to feed (Bejarano et al. 2004, Hendler et al. 2012). Some authors like Neira and Cantera (2005) and Lawley et al. (2018) (as *Ophiothela* cf. *mirabilis*) have found that *O. mirabilis* has a preference for octocoral hosts. However, Mantelatto et al. (2016) indicated that in Brazil, area where it is invasive, *O. mirabilis* is an opportunistic and generalist species in relation to host species selection, finding it related to 20 different invertebrates (i.e., *Dysidea etheria* – sponge, *Isostichopus badionotus* – sea cucumber). The relationship between this brittle star and its hosts is considered as commensalism; however, it has been suggested that there may be a negative effect to the host due to the high densities that *O. mirabilis* can present (Mantelatto et al. 2016). Those negative effects may not be directly caused by its feeding on the host, but some authors suggest that it may be related to structural damage due to the increase in the weight of commensals that the host must support, and in the case of the cnidarians with the possible interruption of the extension of the polyps making it difficult to feed and compromising the ability of the octocoral to obtain nutrients (Mantelatto et al. 2016, Thé de Araújo et al. 2018). In northern Chocó, high densities of *O. mirabilis* on the octocorals were observed during April 2016 and in subsequent samplings in 2017 and 2018, but further studies are needed to elucidate the possible negative effect of this relationship to the octocorals in this area. For the Colombian Pacific, *O. mirabilis* has been reported to be associated mainly with the octocoral *Leptogorgia alba* (Cantera et al. 1987, Pardo et al. 1988, Neira and
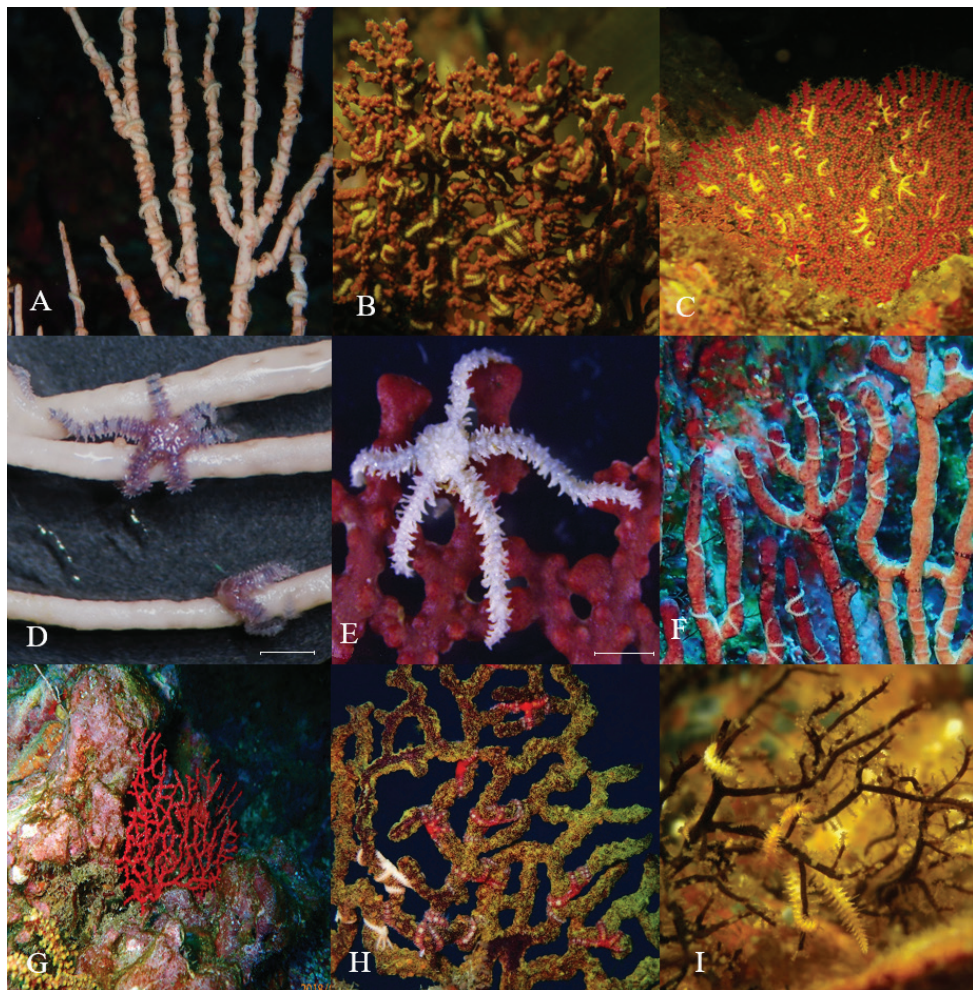
Figure 3. *Ophiothela mirabilis* on different cnidarians **A** *Leptogorgia alba* **B** *Pacifigorgia rubicunda* **C** *P. eximia* **D** *Ophiothela mirabilis* collected on *L. alba* **E** *O. mirabilis* collected on *Pacifigorgia irene* **F** *P. stenobrochis* **G** *P. sculpta* **H** *P. bayeri* **I** Cnidarian. Scale bars: 2 mm (**D, E**).

Cantera 2005). However, the results presented here expand its range of hosts to include other octocoral species: *Pacifigorgia rubicunda*, *P. adamsi*, *P. eximia*, *P. irene*, *P. bayeri*, *P. sculpta*, *P. stenobrochis*, *Muricea squarrosa*, *Samogorgia* sp., and *Leptogorgia* sp., leafy algae, and *E. thouarsii*.

Several individuals of *O. mirabilis* were found using *E. thouarsii* spines as a fixing substrate, but there are no studies of *O. mirabilis* as a sea urchin epibiont in the Tropical Eastern Pacific; however, for the Brazilian Caribbean, where is an invasive species, *O. mirabilis*, has been reported living in high densities in *Echinometra lucunter* spines (Mantelatto et al. 2016). This constitutes the first report of the relationship between *O. mirabilis* and *E. thouarsii*, expanding the range of hosts for *O. mirabilis*.

Beside the groups mentioned above, others organisms have also been reported as *O. mirabilis* hosts, especially in the Mexican Pacific where association with scleractinian corals and sponges have been reported (Granja-Fernández and López-Pérez 2011), and in the Caribbean (Brazil), others groups were found including sponges, ascidians, and bryozoans (Mantelatto et al. 2016). So far there are no other reports of *O. mirabilis* living in seaweeds. Although the species of this group was not identified to species level, this would be the first record of the relationship between *O. mirabilis* and seaweeds.

Ophionereis annulata (Le Conte, 1851) – *Malmgreniella* cf. *variegata*
Figure 4

Material: two polychaetes of the family Polynoidae identified as *Malmgreniella* cf. *variegata* were found living on specimens of *Ophionereis annulata* collected in Chicocora (CHIC) (INV EQU4370) and Parguera (PARN) (INV EQU4208) (Figure 1). The polychaetes had a similar coloration pattern to the dorsal side of the ophiuroid arms (Figure 4).

The association between polychaetes of the family Polynoidae with brittle stars belonging to the genus *Ophionereis* has been reported for the Pacific Ocean and the Caribbean Sea. *Malmgreniella variegata* (Treadwell, 1917) distributed mainly in the western Atlantic, including the Caribbean Sea (GBIF 2019, OBIS 2018) has a relationship with *Ophionereis reticulata* (Say, 1825) (Hendler et al. 1995). This association has been well described for Brazil (Santa-Isabel et al. 1996) and recently for Venezuela (Gómez-Maduro and Díaz-Díaz 2017). *Malmgreniella variegata* has a similar coloration and a banded pattern as the ophiuroid arms, which allows it to go unnoticed on the host (Pettibone 1993, Gómez-Maduro and Díaz-Díaz 2017). *Malmgreniella* cf. *variegata* has been reported mainly associated with the aboral part of the disk of the ophiuroid, using it as a refuge (Granja-Fernández et al. 2013). Although *M. variegata* is distributed in the Atlantic Ocean, some authors such as Pettibone (1993) reported the species living on *Ophionereis annulata* in the Gulf of Panama. In the Mexican Pacific, Granja-Fernandez et al. (2013) described a similar commensal relationship between *O. annulata* and a polynoid polychaete, which, after reviewing its morphology, was identified as *M.* cf. *variegata*, due to differences in the color pattern of the elytra and the notochaetae from *M. variegata* from the Caribbean Sea. After examination of the specimens collected in northern Chocó we found all the taxonomic characteristics described by Salazar-Silva (2009) for the Atlantic polychaete *Malmgreniella variegata* except for the color pattern of the elytra, similar to the results described by Granja-Fernandez et al. (2013). The identification of these polychaetes needs to be revised using additional evidence, such as molecular analysis. This is the first report of the presence of *M.* cf. *variegata* and its association with *O. annulata* in the Colombian Pacific.

Figure 4. *Malmgreniella* cf. *variegata* (left) and *Ophionereis annulata* (right). Scale bar: 5 mm.

Eucidaris thouarsii (L. Agassiz y Desor, 1846) – Bryozoa, Cirripedia, *Suberites* aff. *ficus*, and *Ophiothela mirabilis* Verrill, 1867
Figure 5

Material: Four types of epibionts were found inhabiting on *Eucidaris thouarsii* spines in different stations (Figure 1), including cirripede barnacles (INV EQU4218), several species of bryozoans (INV EQU4528, INV EQU4293, INV EQU4299) (Figure 5A), and the sponge *Suberites* aff. *ficus* (INV EQU4301) in Piedra Zapata (P.ZAP) (Figure 5B). The ophiuroid *O. mirabilis* was collected on the sea urchin (INV EQU4218) in Coló (COLO) and Piedra de Eroito (P.ERO) (Figure 5C, D).

Only one sea urchin morphotype belonging to the family Cidaridae was found in the rocky reefs in northern Chocó, identified as *Eucidaris thouarsii*, mostly due to its thick spines (Figure 5). Different organisms use *E. thouarsii* spines as an attachment substrate, including sessile (bryozoans, sponges) and mobile animals (*O. mirabilis*). There are not many published papers related to the epibionts species of sea urchins; however, it has been reported that sponges, especially species belonging to the genus *Clathria*, grow on the spines and the discs of *E. thouarsii* (David et al. 2009, Aguirre et al. 2011). For other species of sea urchin, different associations have been reported: for *H. asteriscus* more than 20 species of epifauna have been identified, including nine

Figure 5. Epibionts on *Eucidaris thouarsii* spines **A** Bryozoans **B** *Suberites* aff. *ficus* **C** *Ophiothela mirabilis* **D** close up to *O. mirabilis* collected from *E. thouarsii* spine.

species of polychaetes, five species of bryozoans, three species of mollusks, three species of crustaceans, two sponge species, and a single species each of protozoan, cnidarian, nematode, and echinoderm (Salazar and López 1983). The reason sea urchins of the family Cidaridae are commonly used as hosts is that they have spines made of muscle and collagen in their basal part which allows the settlement of epibiont fauna, unlike other echinoids which have antifouling compounds (David et al. 2009, Aguirre et al. 2011). In this work, the sponge that settled on *E. thouarsii* spines was identified as *Suberites* aff. *ficus* (Figure 5B) because of the spicules. *Suberites ficus* (Johnston, 1842) is the given name for a complex of species with megascleres, tylostyles, microscleres, strongyles, and oxeas, originally from the North Atlantic Ocean but with two records on the eastern Pacific (Dickinson 1945, Bakus and Green 1987). The tylostyles and

microscleres from the Colombian Pacific specimen are smaller (tylostyles: 90–221 × 3–8 μm; microscleres: 17–42 × 1–3 μm) than the ones reported in specimens from other areas of the Eastern Pacific, such as lower California, Mexico (tylostyles: 340 × 10 μm; microscleres: 18–36 × 1–3 μm; De Laubenfels 1932) and south California (tylostyles: 120–680 × 1–11 μm; microscleres: 20–48 × 1–2.5 μm; Bakus and Green 1987). Until now, *Clathria* was the only sponge genus reported growing on *E. thouarsii* (Aguirre et al. 2011), but *S. ficus* has been reported living on other organisms such as gastropod shells (Bakus and Green 1987). This report constitutes the first record of *S.* aff. *ficus* and its association with *E. thouarsii* for the Colombian Pacific. At least five unidentified bryozoan species (Figure 5A) have been observed on the spines of *E. thouarsii*, which were collected in parts of the study area (INV EQU4528, INV EQU4293, INV EQU4299).

The phylum Crustacea is another of the groups reportedly associated with sea urchins; different species, especially of crabs and shrimps, have been found living between the spines and, in some cases, attached to the spines (Macía and Robinson 2012, Britayev et al. 2013), using the spines as protection and on occasion benefiting from the sea urchin's grazing (Morton 1988). However, there is not much information about other crustaceans, especially about barnacles symbiotic with sea urchins. Some species that have been reported living in sea urchin spines are *Balanus trigonus* and *Paralepas percarinata* (as *Heteralepas percarinata*) (Werner 1967, Aldous 1970).

Diadema mexicanum A. Agassiz, 1863 – *Echineulima* cf. *robusta* (Pease, 1860)
Figure 6

Material: Three specimens of *Echineulima* cf. *robusta* were found on the oral portion of one specimen of the sea urchin *Diadema mexicanum* (INV EQU4292), and five organisms were found on another specimen (INV EQU4530). Both sea urchins were juveniles (INV EQU4292, 18.6 mm test diameter; INV EQU4530, 25.4 mm test diameter). The specimens were collected in Piedra de Jairo (P.JAI) (INV EQU4292) and La Foca (FOCA) (INV EQU4530) (Figure 1). The gastropods were white in color (Figure 6).

The associations between echinoderms and gastropods have been widely recorded for the family Eulimidae, including 750 species (Warén 1983, Jangoux 1984). For the species *Centrosthepanus coronatus* it was reported that they have an ectoparasitic relationship with gastropods of the genus *Echineulima* (Jangoux 1984, Cantera and Neira 1987). These gastropods parasitize the interambulacral zone on the oral side of the test, using a proboscis that penetrates the skeleton to feed on the hemal fluid of its host (Cantera and Neira 1987). This relationship is considered as parasitism because of the damage caused by the gastropod to the sea urchin; among the negative effects that have been recorded for these gastropods, in addition to the fact that they feed on the sea urchin, they produce lesions by their grip, causing dermal swellings and even distor-
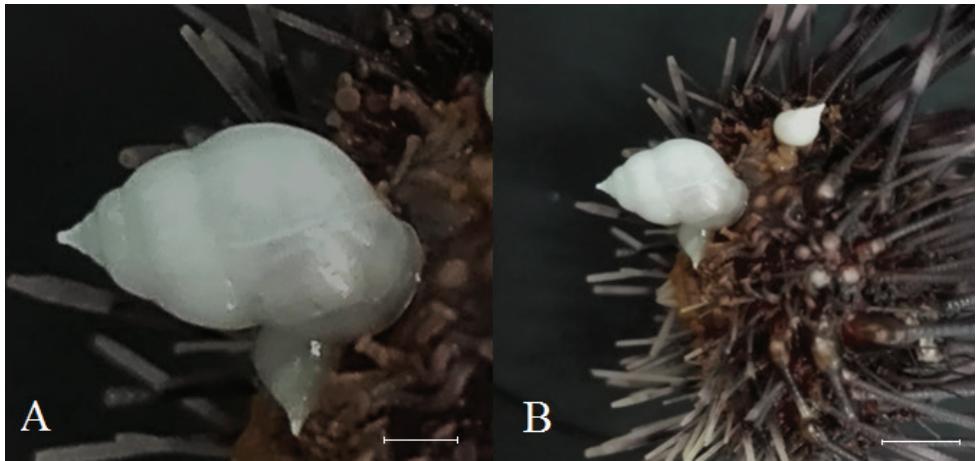
Figure 6. A *Echineulima* cf. *robusta* **B** *Diadema mexicanum* (INV EQU4292) with three specimens of *Echineulima* cf. *robusta*. Scale bars: 2 mm (**A**), 4 mm (**B**).

tion in the skeleton (Jangoux 1984). In the present work two individuals of *Diadema mexicanum* were collected with several individuals of *Echineulima* cf. *robusta* present on the oral side, close to the mouth (Figure 6). *Echineulima robusta* has already been registered as parasite of the sea urchins of the same family in the Indo-Pacific (Warén 1983); however, for the Colombian Pacific Cantera and Neira (1987) reported *Echineulima* sp. parasitizing *C. coronatus* for Gorgona Island. Other species of *Echineulima* have been reported parasitizing sea urchins in other geographical areas, such as in the Gulf of California (Mexico) and Taboga islands (Panama) where the association between *D. mexicanum* and *Echineulima mittrei* (Petit de la Saussaye, 1851) has been observed (Lützen and Nielsen 1975, Alvarado et al. 2015), and in Hawaii where *Echineulima thanuumi* (Pilsbry, 1921) has been reported parasitizing sea urchins of the genus *Echinotrix* (Cantera and Neira 1987). Olivares-González (1986) found that there exists a preference of the parasite *E. mittrei* for sea urchins with test diameters of approximately 20 mm to 39 mm, although the gastropod was found in sizes ranging from 20 mm to 60 mm. These preferences are related to the energy expenditure; in other words, sea urchins smaller than 20 mm use their energy for body growth while larger animals use it to produce gametic material, which is the presumably the preferred source of food for the gastropod.

Three specimens of *Echineulima* cf. *robusta* were found on one of the sea urchins of *Diadema mexicanum*, and five on the other; however, in this last one the gastropods were found in the oral side of the test separated in what looked like two different groups: the first group had three individuals, one of them bigger than the other two, and the other group had two individuals similar in size. Olivares-González (1986) found that sea urchins with more than one individual have them organized in groups of one female and one or two males; the males sharing a single impression on the test but with different apertures. Although the association between gastropods of the genus *Echineulima* with other sea urchins has already been reported for Gorgona Island (Cantera and Neira 1987), this report constitutes the first report for the Colombian
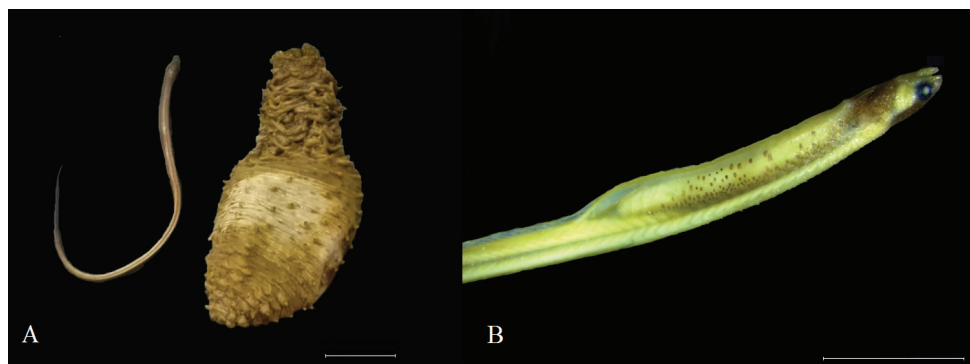
Figure 7. A *Holothuria impatiens* (right) and *Encheliophis vermicularis* (left) **B** Close up of *E. vermicularis*. Scale bars: 8 mm (**A**), 5 mm (**B**).

Pacific of *Echineulima* cf. *robusta* and its relationship with *Diadema mexicanum*. Additionally, in this work we are reporting that *Echineulima* cf. *robusta* can parasitize smaller sea urchins (18.6 mm test diameter) than previously reported.

Holothuria (*Thymiosycia*) *impatiens* (Forskål, 1775) – *Encheliophis vermicularis* Müller, 1842
Figure 7

Material: One specimen of *Encheliophis vermicularis* (Figure 7) was found inside of one specimen of *Holothuria* (*Thymiosycia*) *impatiens* (INV EQU4240), collected in Punta Arusí (P.ARU) (Figure 1). The fish measured 58.76 mm length.

The family Holothuriidae serves as host to several species of pearl fish of the family Carapidae (Luciano et al. 2002). In this family it has been found that the genera *Onuxodon* and *Carapus* act as commensals of the sea cucumbers but feed outside their hosts (Parmentier and Vandewalle 2003, Parmentier et al. 2016), while the genus *Encheliophis* behaves like a parasite, staying and feeding on internal tissues, causing small internal wounds and reducing the gonadal tissues of the host (Parmentier and Das 2004, Parmentier et al. 2006). In this work a specimen of *Encheliophis vermicularis* was found inside of *Holothuria* (*Thymiosicia*) *impatiens*. These fish usually dwell in the respiratory or digestive cavities of sea cucumbers, using them as protection and as a source of food (Trott 1981, Luciano et al. 2002, González-Wangüemert et al. 2014), and in some cases where pearl fish are found in pairs, the sea cucumber also serves as a breeding site (González-Wangüemert et al. 2014). The relationship between the genus *Encheliophis* with sea cucumbers has been reported for species such as *Holothuria* (*Microthele*) *fuscopunctata* Jaeger, 1833, *Holothuria* (*Holothuria*) *tubulosa* Gmelin, 1791, and *Isostichopus fuscus* (Ludwig, 1875), amongst others (Parmentier and Vandewalle 2005, Purcell et al. 2016). Regarding *E. vermicularis*, some authors found that it has a very specific rela-

tionship with *Holothuria* (*Mertensiothuria*) *leucospilota* (Brandt, 1835) (Miyazaki et al. 2014), *Holothuria* (*Mertensiothuria*) *hilla* Lesson, 1830 (James 1995) and with lower incidence with *Holothuria* (*Halodeima*) *atra* Jaeger, 1833 (Smith 1964). Although this fish species has already been reported for Gorgona Island as *Encheliophis hancocki* (Reid, 1940) (Reid 1940, Orrell and Hollowell 2018), a synonymized name of *E. vermicularis* (Froese and Pauly 2018), this work expands its distribution to the northern Chocó.

Conclusions

Despite echinoderms constituting an important group with representatives present in all marine ecosystems, and many different kinds of interaction with other phyla have been described, the information on their associations for the Colombian Pacific was limited. This work has helped to increase the knowledge on echinoderms and their associations with other groups including fishes, mollusks, polychaetes, cnidarians, and sponges from the rocky reefs of the Colombian Pacific and in general from the Tropical Eastern Pacific.

Ethics approval and consent to participate

These species do not appear as evaluated in the IUCN Red List. Riscales project is part of the Biodiversity and Marine Ecosystems research program of the Instituto de Investigaciones Marinas y Costeras of Colombia (INVEMAR), which belongs to the Ministry of Environment and Sustainable Development of Colombia, in accordance with Law 99 of 1993 (Article 18), which does not require Permission of Collection of specimens for Scientific Research according to the decree 1076 of 2015 (Chapter 8, Section 1, Article 2.2.2.8.1.2., Paragraph 1).

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RESEARCH ARTICLE

Two new species of socially parasitic *Nylanderia* ants from the southeastern United States

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Abstract

In ants, social parasitism is an umbrella term describing a variety of life-history strategies, where a parasitic species depends entirely on a free-living species, for part of or its entire life-cycle, for either colony founding, survival, and/or reproduction. The highly specialized inquiline social parasites are fully dependent on their hosts for their entire lifecycles. Most inquiline species are tolerant of the host queen in the parasitized colony, forgo producing a worker caste, and invest solely in the production of sexual offspring. In general, inquilines are rare, and their geographic distribution is limited, making it difficult to study them. Inquiline populations appear to be small, cryptic, and they are perhaps ephemeral. Thus, information about their natural history is often fragmentary or non-existent but is necessary for understanding the socially parasitic life history syndrome in more detail. Here, we describe two new species of inquiline social parasites, *Nylanderia deyrupi* **sp. nov.** and *Nylanderia parasitica* **sp. nov.**, from the southeastern United States, parasitizing *Nylanderia wojciki* and *Nylanderia faisonensis*, respectively. The formicine genus *Nylanderia* is large and globally distributed, but until the recent description of *Nylanderia deceptrix*, social parasites were unknown from this genus. In addition to describing the new social parasite species, we summarize the fragmentary information known about their biology, present a key to both the queens and the males of the *Nylanderia* social parasites, and discuss the morphology of the social parasites in the context of the inquiline syndrome.

Keywords

Formicidae, inquiline syndrome, inquilinism, myrmecosymbiosis, social parasitism

Introduction

Ant social parasites exploit the social colony structure of free-living ant species, and they rely on their hosts for colony founding, survival, and reproduction for at least a part, and frequently the entirety of their life-cycles (Hölldobler and Wilson 1990; Buschinger 2009). Social parasitism is a life history strategy exhibited by at least 300 species among the approximately 13,500 described extant ant species. Traditionally, three main types of social parasitism have been recognized: temporary, dulotic, and inquiline social parasitism (Wasmann 1891; Wheeler 1910; Bourke and Franks 1991; Buschinger 2009). Inquilinism has evolved independently many times in the ants, and approximately 100 species are known from at least 30 ant genera which are distributed across six different subfamilies of the formicoid clade. Most inquilines do not produce a worker caste, and instead they invest their reproductive effort in producing sexual offspring. Many inquilines have convergently evolved a suite of similar morphological characteristics known as the "inquiline syndrome" (*sensu* Kutter 1968; Wilson 1971). These shared characteristics often include: elongated antennal scapes, reduced mouthparts, reduced body size, smooth and shiny cuticle, reduction or absence of the worker caste, intranidal mating with close relatives (i.e., adelphogamy), and polygyny (Kutter 1968; Wilson 1971, 1984; Hölldobler and Wilson 1990; Radchenko and Elmes 2003; Rabeling and Bacci 2010; Rabeling et al. 2015, 2019; Bharti et al. 2016). Interestingly, independently evolved inquiline species exhibit a mosaic of inquiline syndrome characteristics, frequently converging on a similar albeit not identical parasitic phenotype (Wilson 1984; Radchenko and Elmes 2003; Rabeling and Bacci 2010; Rabeling et al. 2019).

The genus *Nylanderia* is a member of the ant tribe Lasiini in the subfamily Formicinae (Blaimer et al. 2015) and presently consists of 150 described taxa (Bolton 2019; LaPolla and Kallal 2019). The genus is globally distributed, with the majority of species being found in warm, forested regions, though it is largely absent from the temperate regions of the Palearctic (LaPolla et al. 2011; Bolton 2019; LaPolla and Kallal 2019). In the Nearctic region, 14 native and six introduced species are recognized (LaPolla et al. 2010; Kallal and LaPolla 2012), representing a rather modest fauna given the high diversity and large biogeographic extent of the genus. Until recently, social parasitism was unknown in *Nylanderia* ants, and the first inquiline social parasite in the genus, *Nylanderia deceptrix* (Messer et al. 2016), was described from Massachusetts.

Here, we describe two new *Nylanderia* inquiline social parasites from the Nearctic and provide keys for identifying them. In addition, we summarize our current knowledge about the biology and natural history of these social parasites, and we briefly discuss the species morphologies and life histories in the context of the inquiline syndrome as well as inquiline evolutionary biology.

Materials and methods

Material examined

ABS   Archbold Biological Station, Venus, FL, USA;
MCZC Museum of Comparative Zoology Collections, Harvard University, Cambridge, MA, USA;
SIBR   Social Insect Biodiversity Repository, Arizona State University, Tempe, AZ, USA;
USNM National Museum of Natural History, Washington, DC, USA.

Morphological analysis

Specimens were measured at the MCZ using a Wild M5A stereomicroscope (100× magnification) fitted with an ocular micrometer. Measurements were recorded and rounded to the nearest 0.01 mm at the highest magnification possible for each measurement and specimen. Composite images were generated at ASU using a Leica DFC450 digital camera mounted to a Leica M205 C stereomicroscope and assembled using Leica Application Suite (Version 4.5) and Helicon Focus (Version 6.6.1) software packages. Measurement terminology, abbreviations, and definitions follow LaPolla et al. (2011) and Kallal and LaPolla (2012):

EL   (Eye Length): maximum length of compound eye in full-face view;
GL   (Gaster Length): the length of the gaster in lateral view from the anteriormost point of the first gastral segment (third abdominal segment) to the posteriormost point (in males this included through the posterior end of parameres);
HL   (Head Length): the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin to a line drawn across the posterior margin from its highest points (to accommodate species where the posterior margin is concave);
HW   (Head Width): the maximum width of the head in full-face view (in males, portion of the eyes that extends past the lateral margins of the head is included);
MMC   (Mesonotal Macrosetae Count): the number of erect macrosetae on mesonotum to one side of sagittal plane;
MtMC (Metanotal Macrosetae Count): the number of erect macrosetae on metanotum to one side of sagittal plane;
MW   (Mesonotal Width): the maximum width of the mesonotum in dorsal view;
PW   (Pronotal Width): the maximum width of the pronotum in dorsal view;

PDH (Propodeum Height): height of the propodeum as measured in lateral view from the base of the metapleuron to the maximum height of the propodeum;

PFL (Profemur Length): the length of the profemur from its margin with the trochanter to its margin with the tibia;

PFW (Profemur Width): the maximum width of the profemur;

PL (Paramere Length): the maximum length of the paramere;

PMC (Pronotal Macrosetal Count): the number of erect macrosetae on pronotum to one side of sagittal plane;

SL (Scape Length): the maximum length of the antennal scape excluding the condylar bulb;

SMC (Scape Macrosetal Count): the number of erect macrosetae on the scape visible in full frontal view;

TL (Total Length): HL+WL+GL;

WL (Weber's Length): in lateral view, the distance from the posteriormost border of the metapleural lobe to the anteriormost border of the pronotum, excluding the neck;

CI (Cephalic Index): (HW/HL) × 100;

FI (Profemur Index): (FW/FL) × 100;

REL (Relative Eye Index): (EL/HL) × 100;

SI (Scape Index): (SL/HW) × 100.

Statistical analysis of morphological measurements

To quantify morphological differences characteristic of the inquiline syndrome in *Nylanderia* ants, we collected morphological measurements for social parasites and their hosts and analyzed them statistically. We measured Weber's Length (WL) as a proxy for Total Length (TL) because the gaster of individuals was often damaged during collection. Statistical analyses were conducted using R 3.4.0 (R Core Team 2017) statistical package. Due to low sample sizes that likely contributed to the data being non-normally distributed, we used Kruskal-Wallis tests to determine whether hosts and parasites were significantly different in size. In addition, we applied pairwise Mann-Whitney tests post-hoc to determine individual differences between social parasites and their respective hosts, as well as between the social parasites. A Bonferroni correction was applied to the Mann-Whitney tests to account for multiple comparisons between species and castes, and to provide a more conservative alpha to compensate for low sample sizes in some cases (see below). For the three *Nylanderia* host parasite pairs, we analyzed the following samples: *N. deyrupi*: 29 queens and 5 males; *N. parasitica*: 7 queens and 10 males; *N. deceptrix*: 22 queens and 5 males; *N. parvula* (Mayr, 1870): 19 queens, 13 males, and 15 workers; *N. wojciki* (Trager, 1984): 17 queens, 8 males, and 20 workers; and *N. faisonensis* (Forel, 1922): 17 queens, 10 males, and 29 workers. Morphological measures of *N. deceptrix* were taken during an earlier study (Messer et al. 2016), and we added the morphological measurements of free-living species reported by Kallal and LaPolla (2010) to our dataset.

Morphological examination revealed that the relative forewing length of social parasites is reduced in comparison to the hosts, therefore we measured wing length for *N. deceptrix* (*N* = 22), *N. deyrupi* (*N* = 20), and *N. parasitica* (*N* = 6) individuals and compared them to 128 individuals of 13 non-parasitic *Nylanderia* species, including: *N. arenivaga* (Wheeler, 1905) (*N* = 9), *N. austroccidua* (Trager, 1984) (*N* = 3), *N. bruesii* (Wheeler, 1903) (*N* = 1), *N. concinna* (Trager, 1984) (*N* = 14), *N. faisonensis* (*N* = 12), *N. hystrix* (Trager, 1984) (*N* = 1), *N. magnella* (Kallal & LaPolla, 2012) (*N* = 1), *N. parvula* (*N* = 30), *N. phantasma* (Trager, 1984) (*N* = 4), *N. querna* (Kallal & LaPolla, 2012) (*N* = 6), *N. terricola* (Buckley, 1866) (*N* = 11), *N. vividula* (Nylander, 1846) (*N* = 23), *N. wojciki* (*N* = 13). We calculated the Forewing Index (FWI), which is the ratio of Forewing Length to Weber's Length, to identify the relative wing size of each species. A Kruskal-Wallis test was used to determine if any significant difference in relative wing size was present. Pairwise Mann-Whitney tests, with a Bonferroni corrections, were used to identify significant differences between hosts and parasites. The same analyses were conducted with males of the following species of non-parasitic *Nylanderia* (*N* = 97): *N. arenivaga* (*N* = 5), *N. austroccidua* (*N* = 3), *N. bruesii* (*N* = 19), *N. concinna* (*N* = 12), *N. faisonensis* (*N* = 4), *N .hystrix* (*N* = 4), *N. magnella* (*N* = 3), *N. parvula* (*N* = 15), *N. phantasma* (*N* = 4), *N. querna* (*N* = 4), *N. terricola* (*N* = 12), *N. vividula* (*N* = 8), and *N. wojciki* (*N* = 4). We used all *N. parasitica* males (*N* = 10) in the analyses, but males of *N. deceptrix* and *N. deyrupi* were not included due to the absence of fully formed wings.

Results

Key to the males of Nearctic *Nylanderia* (modified from Kallal and LaPolla 2012)

1	Antennae with 12 segments (Fig. 5A) ....***N. parasitica* sp. nov.**	
–	Antennae with 13 segments **2**	
2	Wings absent or highly reduced (Figs 1D, F; 3C, E)..................................**3**	
–	Wings present and fully developed.... start key from Kallal and LaPolla 2012	
3	Gaster light brown in color similar to mesosoma, REL 27–28, SI 112–121 (Fig. 3C, E)...***N. deyrupi* sp. nov**.	
–	Head and gaster dark brown in color contrasting with light brown mesosoma, REL 34–36, SI 125–127 (Fig. 1D, F).......................................***N. deceptrix***	

Key to the queens of Nearctic *Nylanderia*

1	Scape Index (SI) < 113, Forewing Length > 2.4 mm, 6–7 mandibular teeth ... . **non-parasitic *Nylanderia***	
–	SI ≥ 113, Forewing Length < 2.4 mm, < 6 mandibular teeth **2**	
2	Weber's Length (WL) 0.99–1.07 mm; distinct bicoloration with darker head and gaster (Fig. 1A, C, E) ....***N. deceptrix***	
–	WL < 0.99 mm; head, mesosoma and gaster of uniform color **3**	

3   Mesonotal Macrosetae Count (MMC) 16–23, Metanotal Macrosetae Count
           (MtMC) 6–9, Pronotal Macrosetal Count (PMC) 7–11, and Scape Macro-
           setae Count (SMC) = 0, mandibular dentition absent (Fig. 4A, C, E).........
           .... ***N. parasitica***
–   MMC 10–17, MtMC 2–4, PMC 2–6, and SMC > 0, 3–4 mandibular teeth
           (Fig. 2A, C, E) ....***N. deyrupi***
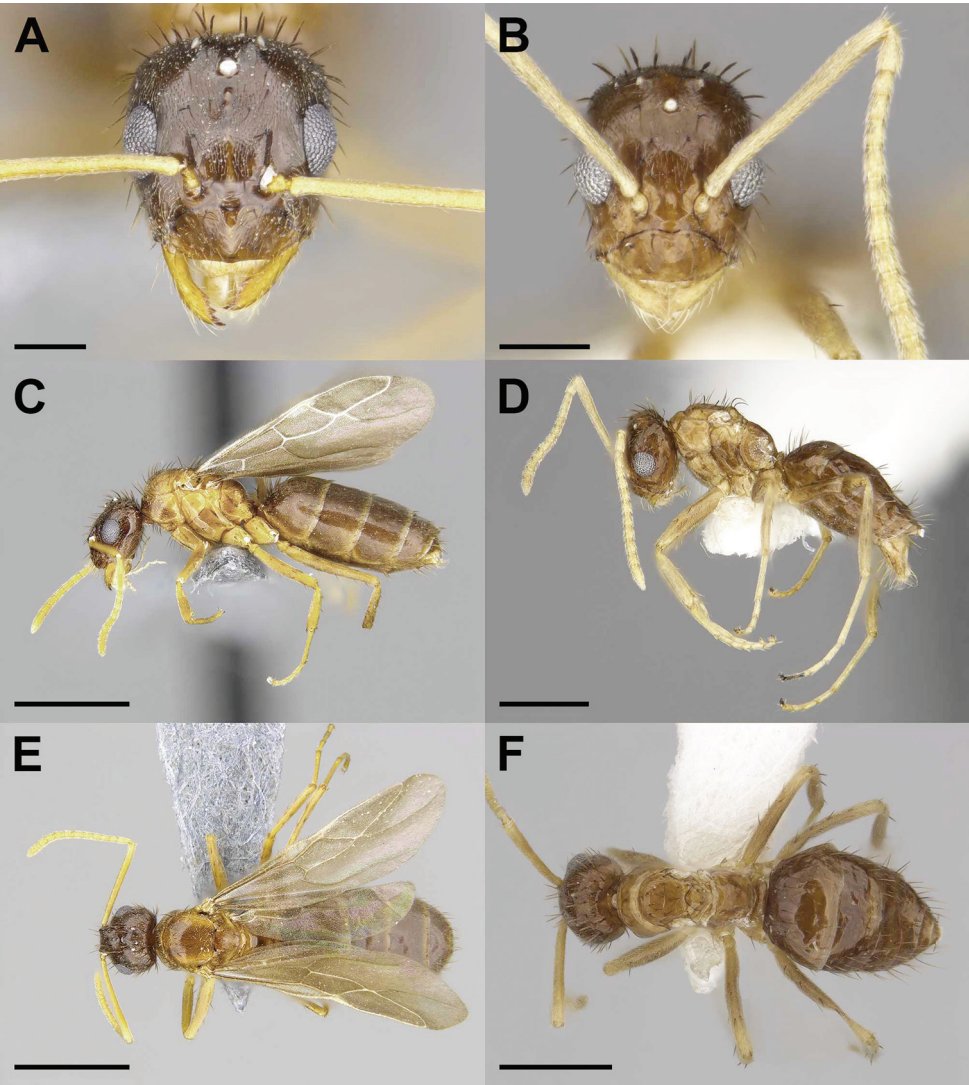

Figure 1. Gyne (**A, C, E**) and male (**B, D, F**) of the previously described social parasite *Nylanderia deceptrix* in full-face (**A, B**), lateral (**C, D**), and dorsal (**E, F**) views. Scale bars: 0.2 mm (**A, B**), 1 mm (**C, E**), 0.5 mm (**D, F**).

Nylanderia deyrupi **sp. nov.**

http://zoobank.org/7F338A9A-2545-4868-844D-D088510F7CDA
Figures 2A, C, E (queen), 3A, C, E (male); see Plate 88 in Deyrup (2016): p. 348.

Material examined. *Holotype*: USA • alate queen; Florida, Highlands Co., Archbold Biological Station; 27.187N, 81.335W, elevation above sea level: 61 m; scrubby flat-woods, slash pine, *Quercus inopina*, *Q. geminata*, Palmetto, *Lyonia lucida*: under leaf-litter of oak canopy at edge gap in pure sand; 15-September-1995; Stefan P. Cover leg.; MCZ-ENT00716681. Deposited at MCZC.

Paratypes: USA • 1 alate queen; same data as for holotype; MCZ-ENT00716678 • 1 male; same data as for holotype; MCZ-ENT00716681 • 1 alate queen, 1 male (on same pin); same data as for holotype; MCZ-ENT00716684 • 1 alate queen, 1 male (on same pin); same data as for holotype; MCZ-ENT00716690 • 1 male; same data as for holotype; MCZ-ENT00716693 • 1 male; same data as for holo-type; MCZ-ENT00716694. MCZ-ENT00716678, MCZ-ENT00716681, MCZ-ENT00716693, MCZ-ENT00716694 deposited at the MCZC; MCZ-ENT00716684, MCZ-ENT00716690 deposited at SIBR.

USA • 1 alate queen; Florida, Highlands Co., Archbold Biological Station; 27.187N, 81.335W, elevation above sea level: 61 m; malaise trap; 6-X-1983; Mark Deyrup leg.; ASUSIBR00000365 • 1 alate queen; same data as previous; but 8-X-1983; ASUSI-BR00000366 • 1 alate queen; same data as previous; but 20-X-1983 ASUSIBR00000367 • 2 alate queens; same data as previous; but 26-X-1983; ASUSIBR00000368–369 • 3 alate queens; same data as previous; but 30-X-1983; ASUSIBR00000370–372 • 2 alate queens; same data as previous; but 15-XI-1983; ASUSIBR00000373–374 • 1 alate queen; same data as previous; but 19-XI-1983; ASUSIBR00000375 • 2 alate queens; same data as previous; but 23-IX-1985; ASUSIBR00000376–377 • 1 alate queen; same data as previous; but 4-X-1985; ASUSIBR00000378 • 1 alate queen; same data as previous; but 9-X-1985; ASUSIBR00000379 • 1 alate queen; same data as previ-ous; but 12-X-1985; ASUSIBR00000380 • 1 alate queen; same data as previous; but 25-XI-1986; ASUSIBR00000381. ASUSIBR00000365-368, ASUSIBR000370-371, ASUSIBR00000373, ASUSIBR00000375-376, ASUSIBR00000378-381 deposited at MCZC; ASUSIBR00000369, ASUSIBR00000372, ASUSIBR00000374, ASUSI-BR00000377 deposited at SIBR.

USA • 3 alate queens; Florida, Highlands Co., Archbold Biological Station; 27.187N, 81.335W; 25-Sept-2010; John LaPolla leg.; JSL100925-1/ASUSIBR00000382–384 • 1 alate queen; same data as previous; JSL100925-2/ASUSIBR00000385 • 1 alate queen; same data as previous; JSL100925-3/ASUSIBR00000386 • 3 alate queens; same data as previous; JSL100925-4/ASUSIBR00000387–389. ASUSIBR00000382, ASUSIBR00000389 deposited at MCZC; ASUSIBR00000383, ASUSIBR00000388 deposited at USMN; ASUSIBR00000384–387 deposited at SIBR.

Diagnosis. A workerless inquiline characterized by small alate queens and apter-ous males. Queens are easily distinguished from host queens by their smaller size

Figure 2. Gynes of the social parasite *Nylanderia deyrupi* (**A, C, E**) and its host *Nylanderia wojciki* (**B, D, F**) in full-face (**A, B**), lateral (**C, D**), and dorsal (**E, F**) views. Scale bars: 0.1 mm (**A, B**), 0.5 mm (**C–F**).

(WL: *N. deyrupi* = 0.79–0.90 vs. *N. wojciki* = 1.10–1.16; Fig. 6), uniformly lighter coloration, long antennal scapes (SI = 118–130 vs. 86–101 in the host), reduced CI (86–94 vs. 95–97 in the host), reduced mandibular dentition (mandible = 3–4 teeth, host = 6 teeth), and reduced macrosetae counts on antennal scapes (2–6 vs. 1–2). In addition, the eyes exceed the lateral margins of the head and hind wing venation is slightly reduced. Males of *N. deyrupi* are completely apterous and are bicolored with a darker head and gaster and lighter mesosoma. The mesonotum is also reduced and narrow from the reduction of flight musculature and does not protrude anteriorly
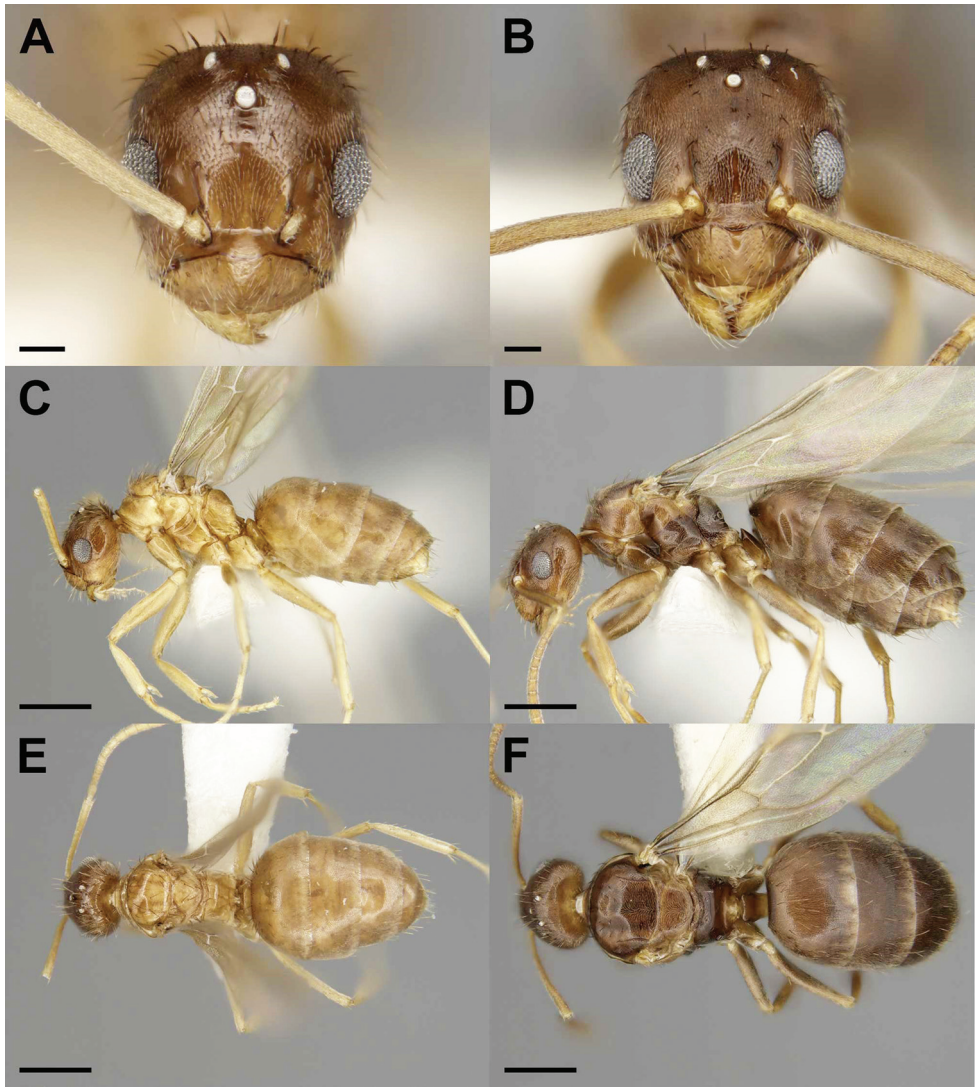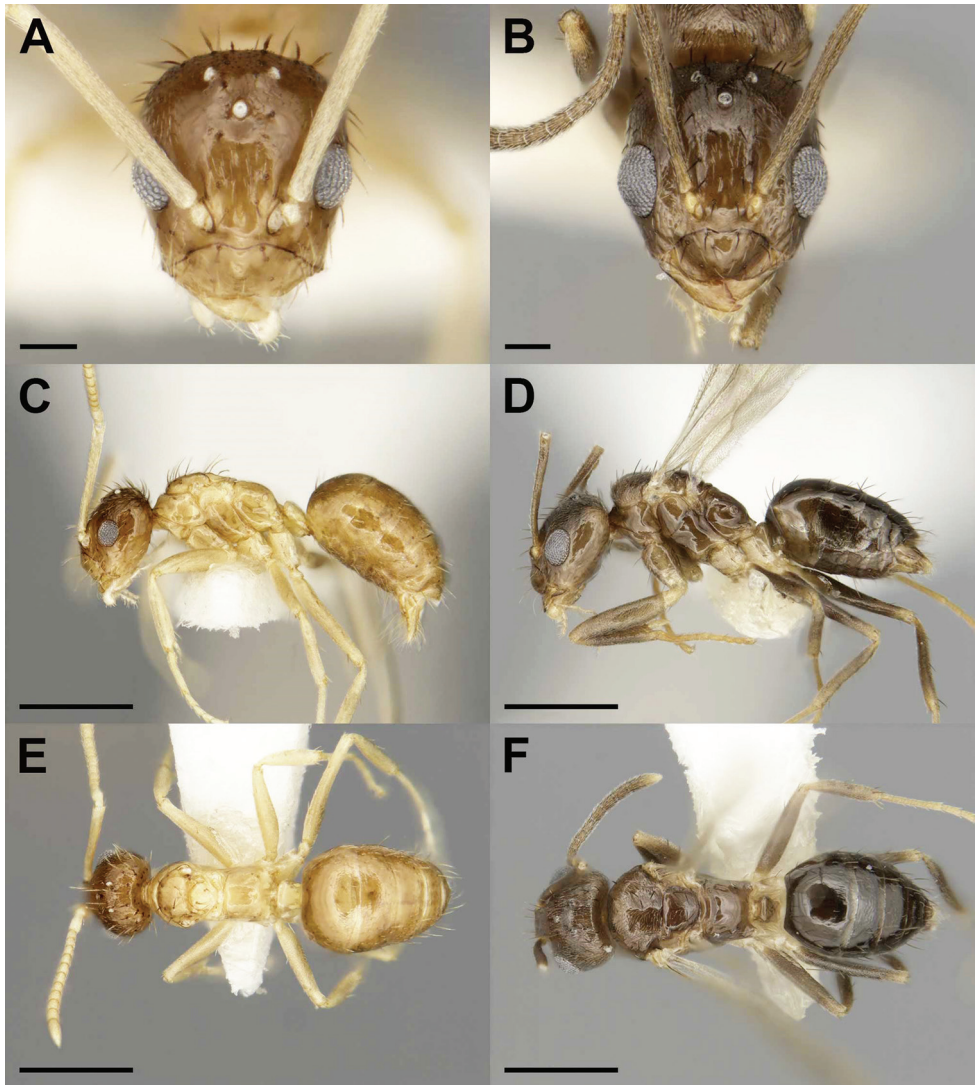
Figure 3. Males of the social parasite *Nylanderia deyrupi* (**A, C, E**) and its host *Nylanderia wojciki* (**B, D, F**) in full-face (**A, B**), lateral (**C, D**), and dorsal (**E, F**) views. Scale bars: 0.1 mm (**A, B**), 0.5 mm (**C–F**).

beyond the pronotum. Host males are fully alate and uniform brown. The antennal scapes lack macrosetae. Reduced REL (27–28 vs. 35–40) and SI increased (112–121 vs. 104–107).

Queens of *Nylanderia deyrupi* differ from those of the closely similar *N. deceptrix* by their smaller overall size (WL: *N. deyrupi* = 0.79–0.90 vs. *N. deceptrix* = 0.99–1.07; Fig. 7), reduced number of macrosetae on the mesonotum (10–17 vs. 21–27), smaller eyes (REL 24–31 vs. 33–37), and uniform coloration (queens of *N. deceptrix* are bicolored). *Nylanderia deyrupi* males are smaller in size (WL 0.55–0.58 vs. 0.66–0.69), possess

more macrosetae on the mesonotum (4–5 vs. 2), pronotal macrosetae are absent, smaller eyes (REL 27–28 vs. 34–36), and shorter antennal scapes (SI 112–121 vs. 125–127).

Description, holotype gyne. *Measurements*: TL 2.68, HW 0.56, HL 0.59, EL 0.17, SL 0.65, MW 0.47, PW 0.57, WL 0.85, GL 1.23, PDH 0.32, PFL 0.69, PFW 0.15, SMC 4, PMC 3, MMC 14, MtMC 3. *Indices*: CI 94, REL 29, SI 118, FI 21. Small size (TL 2.68), body yellow-brown in color, dorsum of head and gaster slightly darker. *Head*: covered in pubescence and macrosetae, slightly longer than wide (CI 94), broadening posteriorly, eyes protruding beyond lateral margins of head, three ocelli present. Maxillary and labial palp formula 6:4, mandibular dentition reduced to apical and three pre-apical teeth. Antennal scapes long (SI 118), exceeding posterior margin of head by length of first three funicular segments, covered in appressed setae with four erect macrosetae. Antennae 12-segmented. *Mesosoma*: dorsum covered with pubescence, largely absent on lateral portions of mesosoma, pronotum bearing three macrosetae, mesonotum bearing 14 macrosetae, metanotum bearing three macrosetae, macrosetae matching body color, macrosetae on metanotum displaying significant curvature towards midline of body. Forewings smaller in size, but not distinctly different from forewings of host, hindwings with slightly reduced venation relative to host. *Metasoma*: gaster covered in pubescence with clusters of macrosetae at anterior portion of first gastric tergite and posteriorly around acidopore.

Measurements, paratype gynes (*N* = 28): TL 2.35–2.88, HW 0.51–0.56, HL 0.58–0.62, EL 0.15– 0.19, SL 0.64–0.67, MW 0.42–0.54, PW 0.42–0.62, WL 0.79–0.90, GL 0.96–1.38, PDH 0.30–0.35, PFL 0.55–0.72, PFW 0.09–0.15, SMC 2–6, PMC 2–6, MMC 10–17, MtMC 2–4. *Indices*: CI 86–94, REL 24–31, SI 118–130, FI 16–24.

Description, paratype males. *Measurements* (*N* = 5): TL 1.80–1.84, HW 0.41–0.42, HL 0.44–0.46, EL 0.12–0.13, SL 0.46–0.50, MW 0.22–0.25, PW 0.28–0.31, WL 0.55–0.58, GL 0.78–0.83, PDH 0.21–0.23, PFL 0.48–0.51, PFW 0.10–0.11, PL 0.20–0.21, SMC 0, PMC 0, MMC 4–5, MtMC 1–2. *Indices*: CI 90–93, REL 27–28, SI 112–121, FI 20–23. Overall yellowish-brown, exhibiting bicoloration with head and gaster darker than mesosoma, yellow color in legs, antennae and mandibles, macrosetae color matching body segment. *Head*: slightly longer than wide (CI 90–93), covered in pubescence and macrosetae, denser posteriorly and laterally, eyes protruding beyond lateral margins of head, three ocelli present. Maxillary and labial palp formula 6:4, mandibular dentition reduced to apical tooth only. Antennal scapes long (SI 112–121), exceeding posterior margin of head by length of funicular segments I–III, covered in pubescence and lacking erect macrosetae. Antennae 13-segmented. *Mesosoma*: small, completely apterous, largely lacking any pubescence. Pronotum lacking macrosetae, mesonotum offset posteriorly from pronotum and rising abruptly possessing four or five macrosetae, metanotum bearing one or two macrosetae that curve towards midline of body. Legs lacking macrosetae. *Metasoma*: petiole triangular with longer posterior face sparsely covered in pubescence, macrosetae present on anterior of first gastral tergite and posterior margins of tergites and sternites. *Genitalia*: parameres narrowly triangular, densely covered in macrosetae, slight mesad curvature at posterior end, digiti narrow and tubular, cuspi broad anteriorly and narrow laterally at posterior end.

Etymology. This species is named in honor of Mark Deyrup, who first discovered the miniature females of *N. deyrupi* in malaise trap samples. Mark Deyrup has been a resident naturalist at Archbold Biological Research Station in Central Florida since 1982, and he is a uniquely gifted natural historian who acquired a phenomenal knowledge about the biology of the ants of Florida. Mark recently synthesized his knowledge in the richly illustrated monograph on the Ants of Florida (Deyrup 2016). His meticulous studies of ant natural history and taxonomy have inspired students and colleagues alike for decades, and without Mark's insightful studies the rich natural history of Florida would be much less explored.

Distribution and natural history. *Nylanderia deyrupi* is a rare, apparently workerless inquiline social parasite occurring only in nests of its host, *Nylanderia wojciki*. It is similar in morphology, and apparently in life-history, to *Nylanderia deceptrix*, the inquiline parasite of *N. parvula*. Its host, *N. wojciki* is native to Florida and the adjacent southeastern states. It is a common ant in sandhill and pine flatwood communities. In contrast, *N. deyrupi* is presently known only from Archbold Biological Station and two areas east of Sebring in Highlands County, Florida (Fig. 9; see also Deyrup 2016), all of which are located on the Lake Wales Ridge in central Florida. This sand ridge is more than one million years old (Turner et al. 2006), and it is home to endemic plants and animals, all narrowly distributed on the ridge itself. Deyrup (2016) suggested that *N. deyrupi* (referred to as *Nylanderia* Species A in Deyrup 2016) may be another such endemic species.

The host, *N. wojciki*, makes small (< 300 workers), usually monogynous colonies nesting in leaf litter or sand, usually in partly or lightly shaded areas (Trager 1984). The nests are often diffuse in the summer months, consisting of multiple shallow chambers within an area of 1–2 square meters, containing workers, brood, and sometimes sexuals. Collections of *N. deyrupi* consisted of queens and males scattered among these small host nest pockets, a pattern extremely similar to that seen in *N. deceptrix* and its host *N. parvula*. A striking feature of its life history, also shared with *N. deceptrix*, is that, unlike many ant inquilines, *N. deyrupi* does not appear to suppress the development of host sexuals. In collections made by M. Deyrup and S. Cover both host and parasite sexuals were commonly found together in the host nest, along with host worker brood and callows, strongly suggesting that the host queen is retained, not eliminated in parasitized colonies, coexisting with the social parasite. Another interesting life-history trait shared with *N. deceptrix* is the production of apterous males, which is unique among *Nylanderia* ants. Accordingly, males have limited mobility and probably no dispersal capability, and mating is expected to occur in or around the host nest (i.e., adelphogamy). Considering the limited mobility and the small number of males present in each nest, inbreeding is expected to occur in *N. deyrupi*. In addition, *N. deyrupi* has a strongly female-biased sex ratio, a phenomenon that has been frequently observed among inquiline social parasites.

Worker caste. *Nylanderia deyrupi* was repeatedly collected from nests of *N. wojciki* and workers of *N. deyrupi* were never encountered. Thus, it is likely that *N. deyrupi* is a workerless inquiline social parasite.

Nylanderia parasitica sp. nov.

http://zoobank.org/DA163361-99CB-47AC-915B-5319A8298A7C

Figures 4A, C, E (queen), 5A, C, E (male); see Plate 89 in Deyrup (2016): p. 349.

Material examined. *Holotype***:** USA • alate queen; Florida, Hamilton Co., 2 miles east of Jasper, Route 6, pine-oak hammock near Snake Pond; 30.533N, 82.883W, elevation above sea level: 41 m; 03-July-1994; M. and S. Deyrup leg.; MCZ-ENT00716663. Deposited at MCZC.

*Paratypes***:** USA • 7 males; same data as for holotype; MCZ-ENT00716664–666, MCZ-ENT00716668, MCZ-ENT00716670–672 • 1 alate queen, 1 male (on same pin); same data as for holotype; MCZ-ENT00716673 • 1 alate queen, 1 male (on same pin); same data as for holotype; MCZ-ENT00716674 • 1 alate queen, 1 male (on same pin); same data as for holotype; MCZ-ENT00716675. MCZ-ENT00716664–666, MCZ-ENT00716668, MCZ-ENT00716673 deposited at MCZC; MCZ-ENT00716670–672, MCZ-ENT00716674–675 deposited at SIBR.

USA • 1 alate queen; Florida, Alachua Co., Gainesville, Rock Creek; 9–17-IX-1983; S. Gupta leg.; MCZ-ENT00716676 • 1 alate queen; same data as previous; but V-1984; MCZ-ENT00716677. MCZ-ENT00716676 deposited at MCZC; MCZ-ENT00716677 deposited at SIBR.

USA • 1 alate queen; Georgia, Jones Co., Piedmont National Wildlife Refuge; 33.05N, 83.7167W; 19–26-VII-1994; J. Pickering leg.; MCZ-ENT00716662. Deposited at MCZC.

Diagnosis. The queen of *N. parasitica* differs from the queen of its host, *N. faisonensis*, by its lightened coloration and smaller size (WL: *N. parasitica* = 0.77–0.83 vs. *N. faisonensis* = 1.00–1.35; Fig. 6). Macrosetae counts across the entire body of *N. parasitica* vs. *N. faisonensis* are higher: MMC (16–23 vs. 4–14), MtMC (6–9 vs. 1–3), and PMC (7–11 vs. 4–6); and macrosetae densely cover the whole gaster. Scape macrosetae are absent. The eyes also extend beyond the lateral margins of the head. Reduced CI (86–91 vs. 91–102), reduced REL (24–26 vs. 30–33), SI increased (113–119 vs. 102–112). Mandibular dentition reduced to an apical tooth and maximally two minute denticles as opposed to six mandibular teeth. Males are distinctly bicolored with a darker head and gaster, and the mesonotum is reduced and does not protrude beyond the pronotum. The pronotum possesses one or two macrosetae, which are absent in *N. faisonensis.* The antennae also have a reduced number of segments, possessing 12 as opposed to 13. CI increased (95–97 vs. 87–94) and reduced REL (26–29 vs. 34–36).

Nylanderia parasitica queens differ from those of *N. deceptrix* by: (i) possessing dense, pale macrosetae across the entire body, (ii) exhibiting a uniform body coloration, and (iii) an overall smaller size (WL: *N. parasitica* = 0.77–0.83 vs. *N. deceptrix* = 0.99–1.07; Fig. 7), (iv) the absence of macrosetae from the antennal scape, (v) reduced profemur size (FI 18–20 vs. 21–24), (vi) smaller relative eye size (REL 24–26 vs. 33–37), and (vii) shorter relative antennal scape length (SI 113–119 vs. 121–130). Mandibular dentition is reduced to an apical tooth and maximally two minute denticles vs. four or five mandibular teeth in *N. deceptrix*. In contrast to *N. deceptrix*, males of *N. parasitica* have (i) fully developed wings, (ii) pale macrosetae across the body, (iii) 1–2

Figure 4. Gynes of the social parasite *Nylanderia parasitica* (**A, C, E**) and its host *Nylanderia faisonensis* (**B, D, F**) in full-face (**A, B**), lateral (**C, D**), and dorsal (**E, F**) views. Scale bars: 0.1 mm (**A, B**), 0.5 mm (**C–F**).

pronotal macrosetae, (iv) a higher number of macrosetae on the metanotum (3–5 vs. 1–2), (v) macrosetae present on the gaster, (vi) a reduced FI (18–20 vs. 22–25), (vii) a reduced REL (26–29 vs. 34–36), (viii) a reduced SI (113–119 vs. 125–127), and (ix) 12-segmented antennae.

Description, holotype gyne. *Measurements*: TL 2.54, HW 0.53, HL 0.59, EL 0.15, SL 0.60, MW 0.49, PW 0.56, WL 0.79, GL 1.16, PDH 0.31, PFL 0.67, PFW 0.14, SMC 0, PMC 9, MMC 16, MtMC 6. ***Indices*:** CI 90, REL 26, SI 114, FI 20. *Nylanderia parasitica* is unique in the context of the Nearctic *Nylanderia* fauna because the queens are the smallest known to date (TL 2.54). ***Head*:** slightly longer than wide
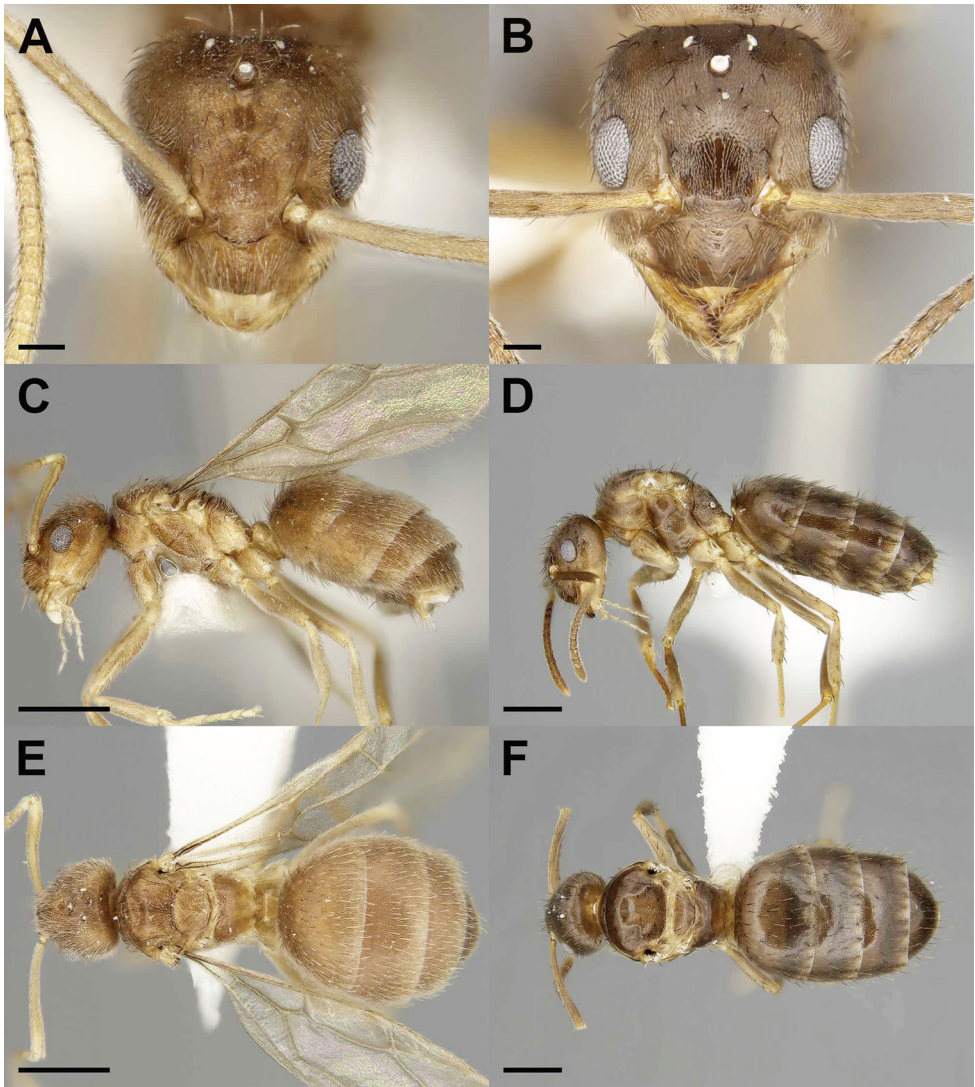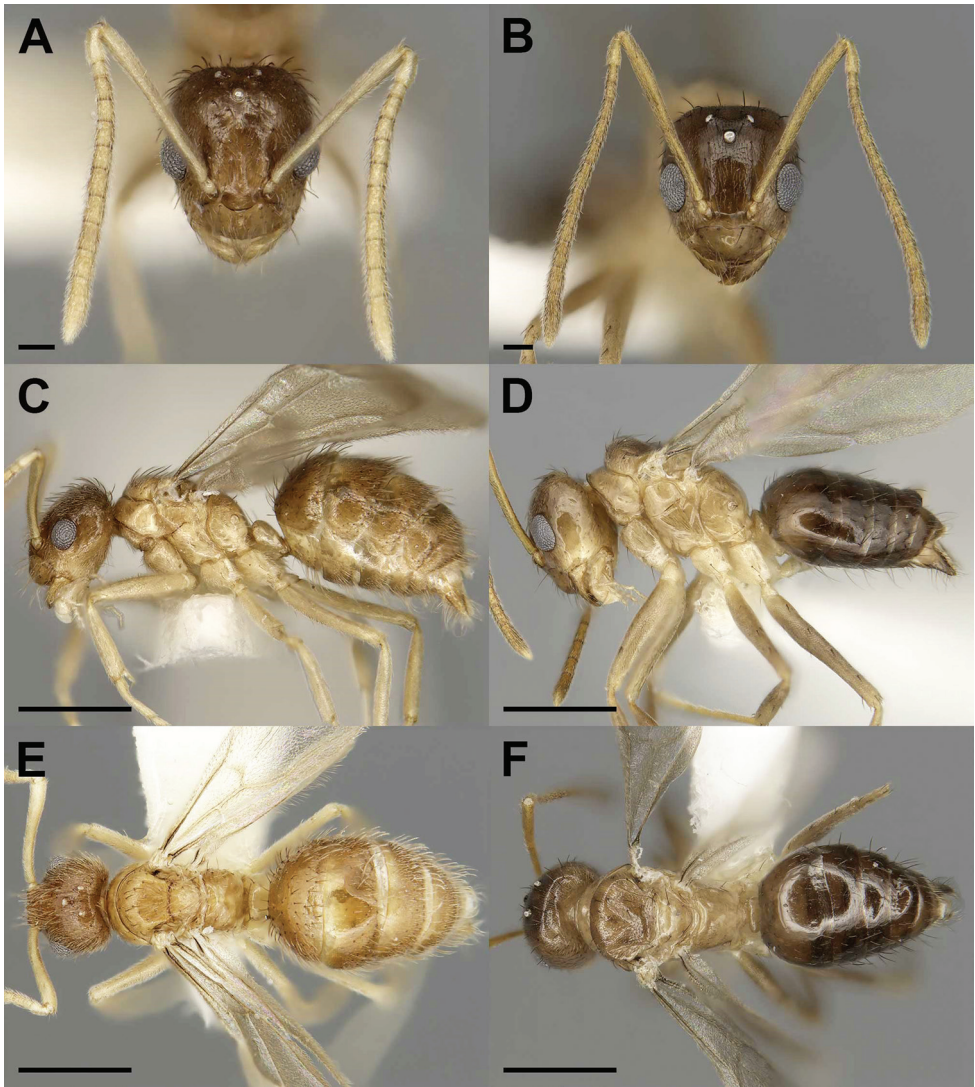
Figure 5. Males of the social parasite *Nylanderia parasitica* (**A, C, E**) and its host *Nylanderia faisonensis* (**B, D, F**) in full-face (**A, B**), lateral (**C, D**), and dorsal (**E, F**) views. Scale bars: 0.1 mm (**A, B**), 0.5 mm (**C–F**).

(CI 90), broadening posteriorly, eyes protruding beyond lateral margins of head, three ocelli present. Maxillary and labial palp formula 6:4, mandibular dentition reduced to apical tooth and one small denticle. Antennae 12-segmented, scapes long (SI 114), exceeding posterior margin of head by length of first three funicular segments, covered in pubescence but lacking macrosetae. **Mesosoma:** fully alate, pronotum bearing nine macrosetae, mesonotum bearing 16 macrosetae, metanotum bearing six macrosetae, mid and hind legs lacking macrosetae. Forewings showing no significant differences in venation from host, slight reduction in venation in hindwings. **Metasoma:** lateral margins of peti-

ole with pubescence and three macrosetae, gaster uniformly covered in dense pubescence and macrosetae. Body uniform yellow-brown in color with legs, antennae, and mandibles lighter yellow. All body regions densely covered in pale pubescence and macrosetae.

Measurements, paratype gynes (*N* = 6): TL 2.27–2.54, HW 0.52–0.56, HL 0.58–0.61, EL 0.15, SL 0.60–0.63, MW 0.44–0.49, PW 0.49–0.57, WL 0.77–0.83, GL 0.89–1.16, PDH 0.30–0.32, PFL 0.60–0.67, PFW 0.11–0.14, SMC 0, PMC 7–11, MMC 16–23, MtMC 6–9. *Indices*: CI 86–91, REL 24–26, SI 113–119, FI 18–20.

Description, paratype males. *Measurements* (*N* = 10): TL 1.70–2.10, HW 0.44–0.47, HL 0.46–0.49, EL 0.12–0.14, SL 0.51–0.54, MW 0.30–0.31, PW 0.36–0.38, WL 0.59–0.64, GL 0.62–0.99, PDH 0.22–0.25, PFL 0.52–0.56, PFW 0.10–0.11, PL 0.15–0.19, SMC 0, PMC 1–2, MMC 10–13, MtMC 3–5. *Indices*: CI 95–97, REL 26–29, SI 113–119, FI 18–20. Body bicolored, pale yellow mesosoma with yellow-brown legs, head and gaster, head slightly darker than gaster, antennae and mandibles yellow. *Head*: covered in pubescence and macrosetae, less dense than in female, slightly longer than wide (CI 95–97), eyes protruding beyond lateral margins of head, three ocelli present; maxillary and labial palp formula 6:4, mandibular dentition reduced to apical tooth only; antennal scapes long (SI 113–119), exceeding the posterior margin of head by length of funicular segments I–III, covered in pubescence, lacking erect macrosetae, antennae 12-segmented, reduced from typical 13-segmented in ants. *Mesosoma*: dorsum covered in pubescence and macrosetae, largely absent on lateral portions of mesosoma, macrosetae matching body coloration, pronotum bearing one or two macrosetae, mesonotum bearing 10–13 macrosetae, metanotum bearing 3–5 macrosetae curving towards the midline of body; fully alate, wings resemble host with no significant differences. *Metasoma*: petiole triangular with longer posterior face, 1–3 macrosetae present; gaster covered in pubescence and macrosetae, with macrosetae clustering on first gastral tergite and posterior margins of tergites and sternites. *Genitalia*: parameres narrowly triangular, straight and densely covered in macrosetae, digiti narrow and tubular, cuspi broad anteriorly and narrow laterally at posterior end.

Etymology. *Nylanderia parasitica* inhabits the nests of *N. faisonensis*, exhibits morphological characteristics of the inquiline syndrome, and potentially lacks a worker caste. Hence, the species epithet is indicative of the socially parasitic life history of *N. parasitica*.

Distribution and natural history. Information on the natural history and biogeography of *N. parasitica* is extremely limited. In previous publications, *N. parasitica* was referred to as undescribed socially parasitic *Nylanderia* species (*N*. sp. 1) (Kallal and LaPolla 2012) and *Nylanderia* Species B (Deyrup 2016). Most individuals of *N. parasitica* were collected from Hamilton County, Florida. Two alate queens were collected from Alachua County, Florida, and a single alate queen was collected from Jones County, Georgia (Fig. 10; see also Deyrup 2016). The type series was collected inside the nest of *N. faisonensis* in a rotten log located in an upland oak-pine hammock and a pond swamp area in Hamilton County (Deyrup 2016). Unfortunately, no additional observations were recorded from this mixed colony. The two queens from Alachua County were collected in malaise traps in May and September, suggesting that *N. parasitica* females disperse on the wing throughout the warm summer months.

The host of *N. parasitica*, *N. faisonensis*, is widely distributed in the southeastern United States (Kallal and LaPolla 2012) and is primarily a woodland species living in rotting branches, under rotting tree bark, or in the leaf litter (Trager 1984). Nests are often fragmented, and they do not make a soil nest like most other Nearctic *Nylanderia* species, with the single queen living deep under the leaf litter, while workers and brood live near the surface (Trager 1984). Alates are reared from August to December, followed by an overwintering period typical of Nearctic *Nylanderia*. Alate individuals disperse from the maternal nests between March and May, while more southern populations start dispersing earlier during those months (Trager 1984). It remains unknown whether *N. parasitica* is tolerant of the *N. faisonensis* queen.

Worker caste. Our limited collections of *N. parasitica* have not yielded any putative workers for this species. Therefore, like *N. deceptrix* and *N. parasitica*, it is likely that this species is a workerless inquiline.

Morphometric analyses

Body size. Reduction of body size is a key characteristic of the inquiline syndrome, and to test the extent of body size reduction in *Nylanderia* social parasites, we compared social parasite queens and males to host queens, males, and workers. In general, queens of socially parasitic *Nylanderia* species were significantly different in body size when compared to host queens and workers (Kruskal-Wallis tests: *N. deceptrix* vs. *N. parvula*, χ^2=37.39, df=2, P=7.6 × 10^{-7}; *N. deyrupi* vs. *N. wojciki*, χ^2 = 56.85, df = 2, P = 4.52 × 10^{-12}; *N. parasitica* vs. *N. faisonensis*, χ^2 = 37.3, df = 2, P = 7.94 × 10^{-9}). Pairwise Mann-Whitney tests revealed that the inquiline queens were significantly smaller than their respective host queens (*N. deceptrix*, P = 5.0 × 10^{-4}; *N. deyrupi*, P = 6.2 × 10^{-7}; *N. parasitica*, P = 6.0 × 10^{-3}) but larger than the host workers (*N. deceptrix*, P = 5.0 × 10^{-4}; *N. deyrupi*, P = 6.2 × 10^{-7}). *Nylanderia parasitica* marked the only exception where no significant size difference was detected between inquiline queens and host workers (P = 0.3; Fig. 6). Comparing the three social parasite queens to each other also revealed a significant size difference between the inquiline species (Kruskal-Wallis test: χ^2 = 31.87, df = 2, P = 1.2 × 10^{-7}; Fig. 7), with *N. deceptrix* being the largest and *N. parasitica* the smallest.

Comparing the social parasite males to the males of their respective host species, *N. deceptrix* and *N. deyrupi* were not significantly different in body size from the host males (Mann-Whitney tests: P = 0.44 and P = 1, respectively). In contrast, *N. parasitica* males were significantly smaller than *N. faisonensis* males (Mann-Whitney test: P = 0.01). When males of the three social parasite species were compared to each other, no significant difference in size was detected (Kruskal-Wallis test: $\chi 2$ = 2.67, df = 2, P = 0.26).

Wing size. Behavioral observations revealed that queens and males of *N. deceptrix* do not mate or disperse on the wing (Messer et al. 2016). Both inside nest mating and a reduced dispersal ability are important life history traits of inquiline social parasites, contributing to their localized distribution and frequently inbred population structure. Therefore, and as a proxy for flight performance, we measured the wings lengths of 13 free-living and three socially parasitic *Nylanderia* species. To test whether the social
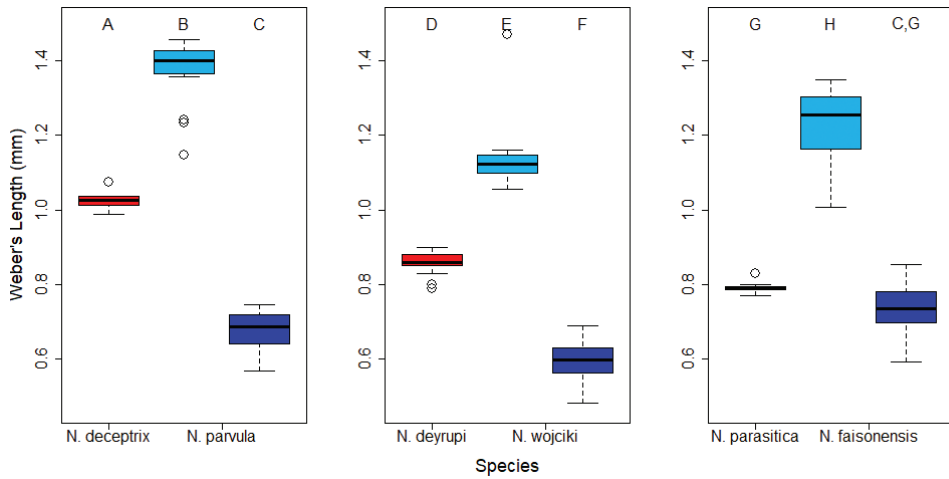
Figure 6. Boxplots comparing body sizes (Weber's Length) of social parasite queens (red) to the queens (light blue) and workers (dark blue) of their respective host species. Letters above the boxes indicate significantly different groups (Pairwise Mann-Whitney Test with Bonferroni correction, P < 0.05).
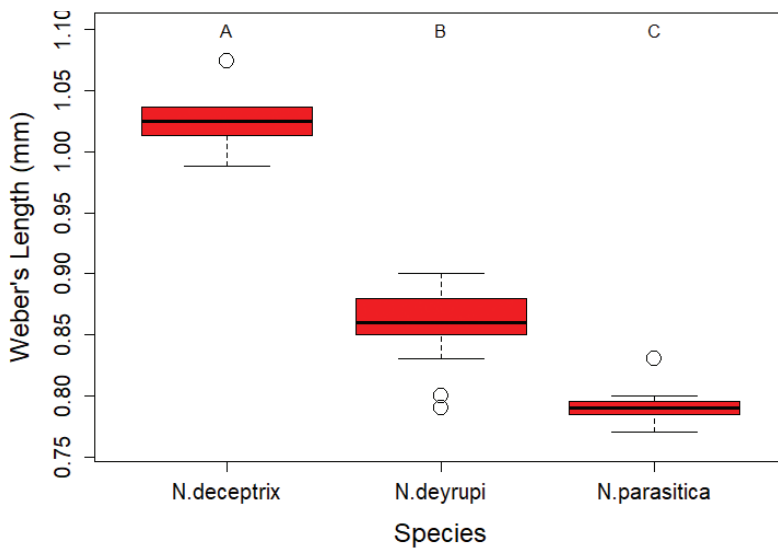
Figure 7. Boxplot comparing body sizes (Weber's Length) of social parasite queens to each other. Letters above the boxes indicate significantly different groups (Pairwise Mann-Whitney Test with Bonferroni correction, P < 0.05).

parasites have shorter relative wing lengths when compared to free-living *Nylanderia* species, we calculated the ratio of Forewing Length to Weber's Length and compared the values across Nearctic *Nylanderia* species for both queens and males. Significant differences between species were detected in both queens (Kruskal-Wallis test: $\chi 2 = 140.46$, df = 15, $P < 2.2 \times 10^{-16}$) and males (Kruskal-Wallis test: $\chi 2 = 71.748$, df = 13, $P = 3.819 \times 10^{-10}$). Pairwise Mann-Whitney tests determined that the wing sizes
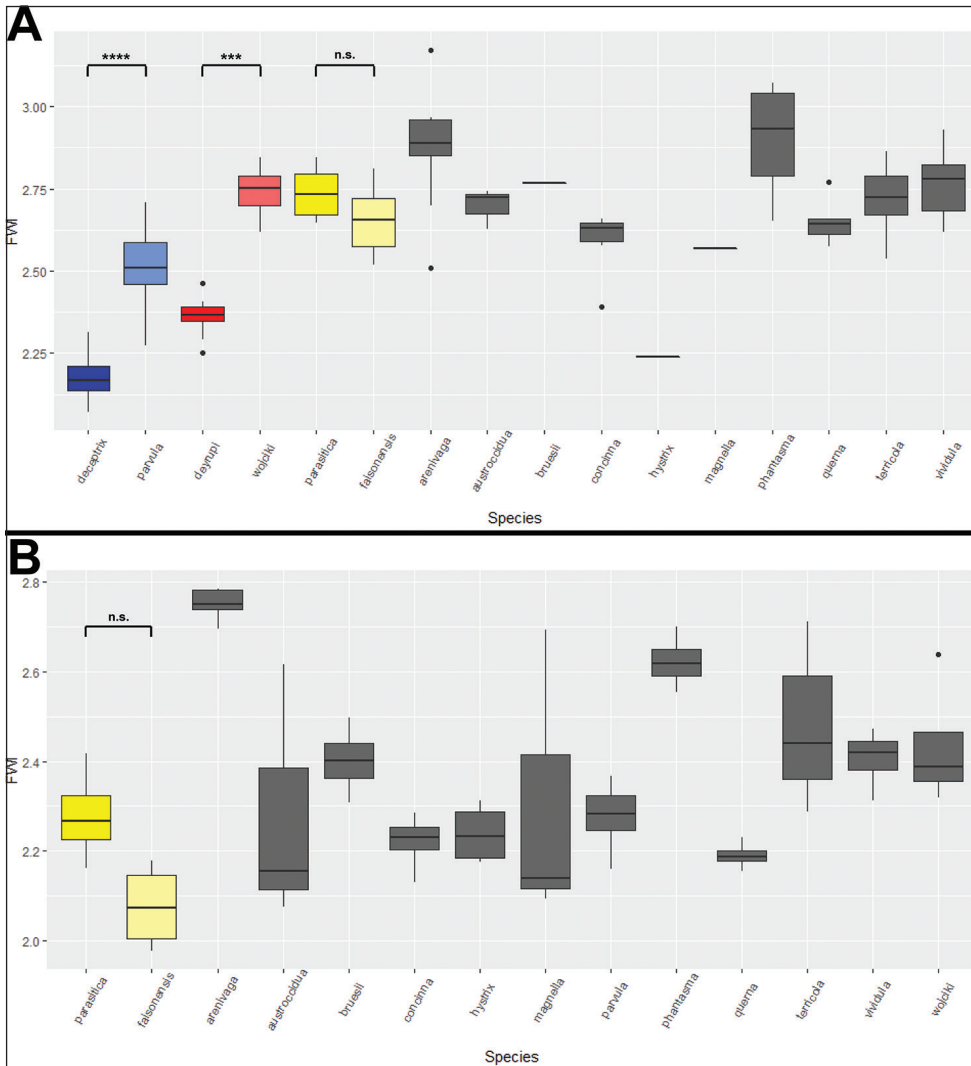
Figure 8. Boxplots of the Forewing Index (FWI) in (**A**) gynes of non-parasitic Nearctic *Nylanderia* (grey), *N. deceptrix* (red), *N. deyrupi* (blue), and *N. parasitica* (yellow), as well as (**B**) males of non-parasitic Nearctic *Nylanderia* (grey) and *N. parasitica* (yellow). Host species are represented by a lighter color shade than their respective social parasite species. (*** = P < 0.001, **** = P << 0.0001).

of *N. deceptrix* and *N. deyrupi* queens were significantly reduced relative to their host species (P = 2 × 10⁻⁷; P = 2.2 × 10⁻⁴, respectively; Fig. 8A). In contrast, both queens and males of *N. parasitica* did not exhibit any significant reduction in wing size relative to the host *N. faisonensis* (Mann-Whitney tests: P = 1; P = 0.364, respectively; Fig. 8B). Males of *N. deceptrix* and *N. deyrupi* were not included in the pairwise analysis, because they are brachypterous and apterous, respectively (Figs 1, 3).

Discussion

We described two new workerless inquiline social parasite species in the genus *Nylanderia*, *N. deyrupi* and *N. parasitica*, from the southeastern United States. *Nylanderia deyrupi* was discovered in nests of *N. wojciki*, and *N. parasitica* was found once inside the nest of *N. faisonensis*. In ants, the presence of mixed colonies is indicative of a socially parasitic life history. *Nylanderia deyrupi* was collected repeatedly at or around Archbold Biological Station in central Florida, which yielded first insights into the biology of the species. In contrast, very little information is known about *N. parasitica*, which was only observed alive once in northern Florida. Therefore, our interpretations regarding the biology of the two species, especially of *N. parasitica*, should be regarded as preliminary and would greatly benefit from additional study. Notwithstanding, first observations suggest that *N. deyrupi* is a workerless, host queen tolerant inquiline because the *N. wojciki* queen, callow workers, and sexual brood were found inside the host colonies, whereas workers of *N. deyrupi* were absent. *Nylanderia parasitica* was only found in a mixed colony with *N. faisonensis*, and at the moment it remains unknown whether this inquiline species is host tolerant or not, but workers of *N. parasitica* were also absent from this mixed colony.

The description of these two social parasite species increases the diversity of Nearctic *Nylanderia* to 17 species, and three of them are inquiline social parasites. Approximately 100 species of inquiline social parasites are known from six ant subfamilies. The majority of the inquiline social parasites belong to the subfamily Myrmicinae, and only 12 inquiline species are known from the subfamily Formicinae, including the genera *Anoplolepis, Camponotus, Cataglyphis, Formica, Nylanderia, Plagiolepis,* and *Polyrhachis* (Hölldobler and Wilson 1990; Buschinger 2009; Karaman 2012; Casevitz-Weulersse 2014; Messer et al. 2016). Considering that inquiline social parasites are less common in formicine ants, these new *Nylanderia* inquiline species provide an opportunity for comparatively studying the morphological, behavioral, and ecological traits associated with inquiline social parasite evolution in formicine ants.

Nylanderia deyrupi and *N. parasitica* seem to have limited geographic distribution ranges, which is typical for inquiline species (Wilson 1971; Buschinger 2009). So far, *N. deyrupi* is known from central Florida (Fig. 9), while *N. parasitica* was collected in northern Florida and southern Georgia (Fig. 10) (Deyrup 2016). These distribution ranges are significantly smaller than the ranges of their respective host species (Figs 9, 10) (Trager 1984; Kallal and LaPolla 2012; Deyrup 2016). However, *N. parasitica* has a considerably larger known range compared to both *N. deceptrix* and *N. deyrupi*. Considering that males of *N. parasitica* are fully winged and that queens were collected in Malaise traps, it is possible that mating and/or dispersal flights occur in this species, which could contribute to a wider geographic distribution. The currently recognized biogeographic distribution almost certainly also reflects sampling biases, considering that inquiline social parasites are rarely found.

Figure 9. Geographic distribution of *N. deyrupi* (black star) and its host *N. wojciki* (red circles). Host distribution data was supplemented with additional information from antmaps.org (Janicki et al. 2016).

The inquiline syndrome of *Nylanderia* social parasites

Social parasites display a mosaic of morphological, behavioral, and life history traits characteristic of their socially parasitic biology, known as the inquiline syndrome (Kutter 1968; Wilson 1971). *Nylanderia* inquiline social parasites show adaptations and losses associated with a socially parasitic life history, including a loss of the worker caste, polygyny, elongated scapes, lighter coloration, reduced body sizes, reduced wings, and a loss of antennal segments (Table 1). Other inquiline syndrome characters outlined by Wilson (1971) and Hölldobler and Wilson (1990), such as reduced labial and/or maxillary palps, a smooth and shiny cuticle, and a reduced pilosity could not be observed in *Nylanderia* social parasites, supporting the hypothesis that morphological, behavioral, and life history traits characteristic of a socially parasitic lifestyle evolve convergently in a mosaic fashion (Wilson 1984; Hölldobler and Wilson 1990; Radchenko and Elmes
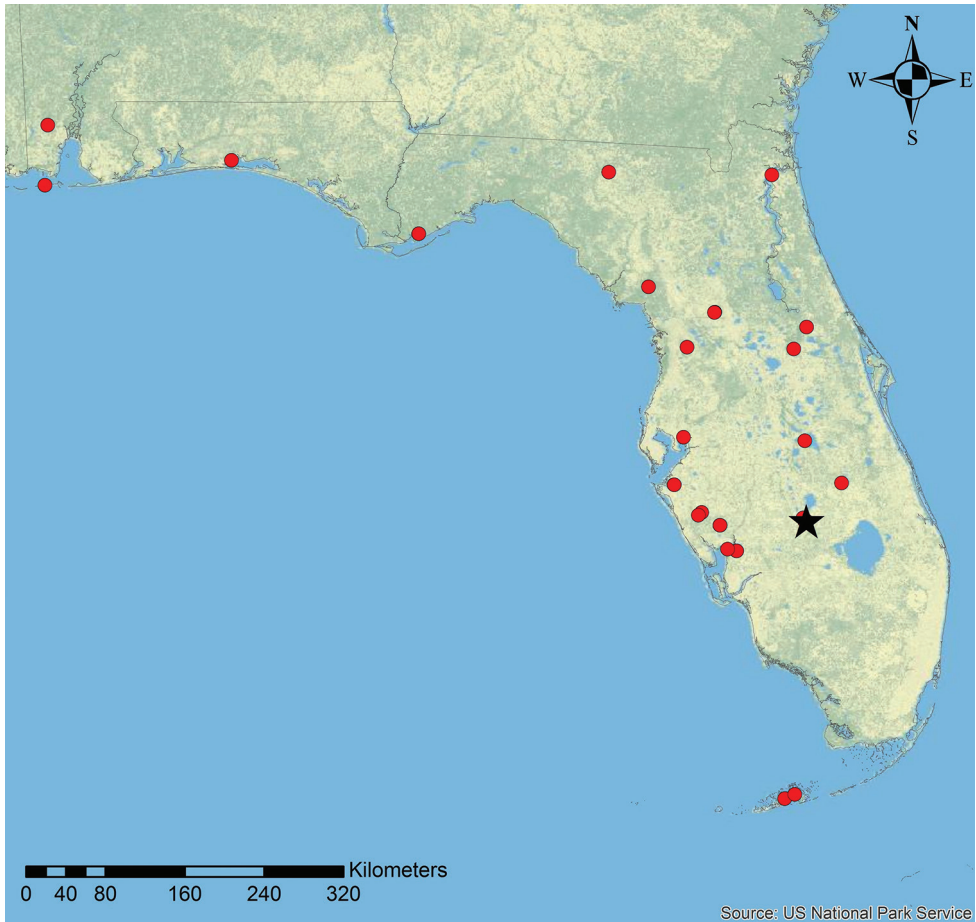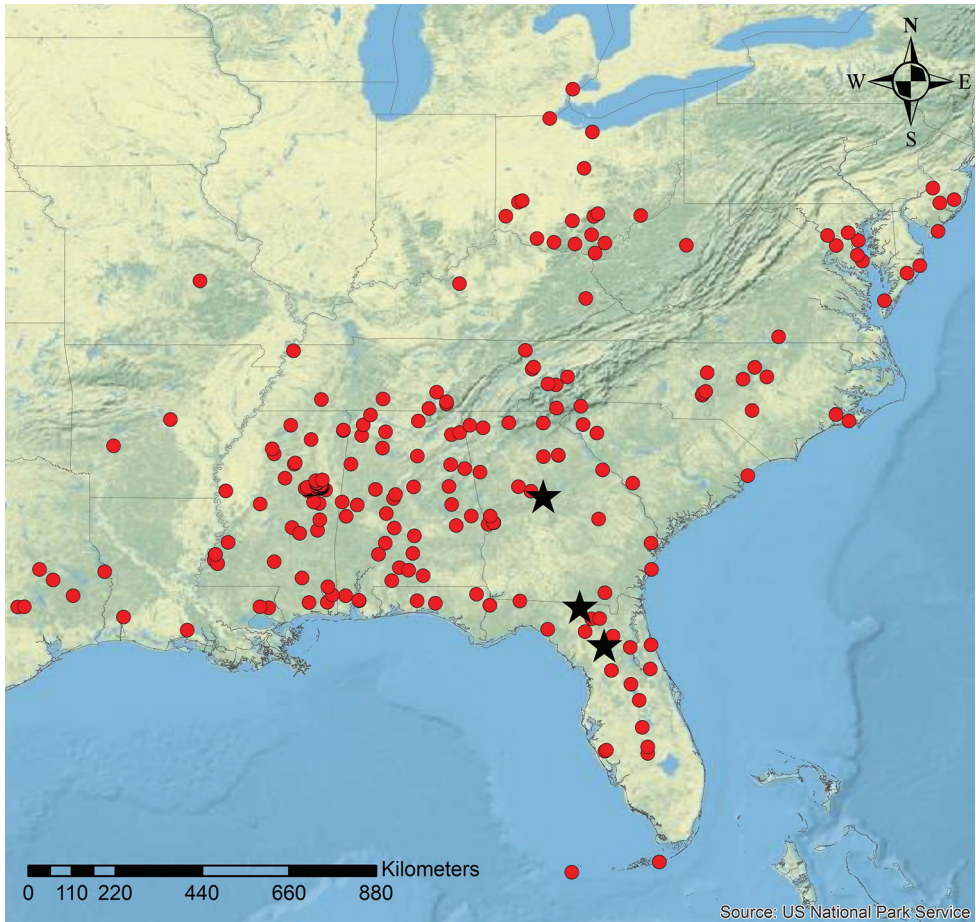
Figure 10. Geographic distribution of *N. parasitica* (black stars) and its host *N. faisonensis* (red circles). Host distribution data was supplemented with additional information from antmaps.org (Janicki et al. 2016).

2003; Rabeling and Bacci 2010; Rabeling et al. 2015, 2019). We briefly discuss the most significant modifications observed in *Nylanderia* inquiline social parasites.

Body size reduction. In comparison to their hosts, all three *Nylanderia* social parasite species are significantly reduced in size. A comparative analysis of the inquiline syndrome in *Pheidole* and fungus-growing ant social parasites revealed that body size reduction is one of the first traits to evolve in inquilines (Wilson 1984; Rabeling and Bacci 2010). Nonacs and Tobin (1992) conducted an analysis of inquiline size relative to their hosts, using head size as a proxy for body size, and discovered that the queens of 18 of the 19 species in their study were equal in size or smaller than the host workers. A behavioral study of *Plagiolepis* inquilines examined the effect of size reduction on social parasite survival, revealing that miniaturization prevented *P. xene* queen and male brood from being culled by host workers (Aron et al. 1999, 2004). In contrast, *P. pygmaea* host males, which are larger than the host workers, were actively removed

Table 1. Comparison of inquiline syndrome characteristics for *N. deceptrix, N. deyrupi*, and *N. parasitica*. Traits applying to females but not males are marked with an asterisk (*), whereas traits applying to males but not females are marked with a cross (·). Morphological reductions observed in social parasites were determined by comparisons relative to the respective host species.

	N. deceptrix	*N. deyrupi*	*N. parasitica*
Loss of worker caste	X	X	X
Presence of multiple parasite queens in host colony (polygyny)	X	X	X
Coexistence with host queen (host-queen tolerance)	X	X	?
Reduced body size	X	X	X
Limited geographic distribution	X	X	X
Reduced wing venation	X	X	–
Reduced mouthparts	–	–	–
Reduced antennal segments	–	–	X·
Smooth, shiny integument	–	–	–
Elongated scapes	X	X	X*
Reduced pilosity	–	–	–
Reduced wings	X	X	–
Reduced mandibular dentition	X	X	X

from the colony (Aron et al. 1999, 2004). In *Nylanderia*, only *N. parasitica* queens are similar in size to the host workers, which is consistent with the pattern observed by Nonacs and Tobin (1992). However, *N. deceptrix* and *N. deyrupi* show a lesser degree of size reduction with both inquiline species displaying intermediate sizes between their respective host queens and workers. It would be insightful to conduct behavioral experiments to test whether a lesser degree of body size reduction in these inquilines increases their risk of being detected and removed by the host.

Wing size reduction. Studying the wing morphology of social parasites is important for inferring the species mating and dispersal behavior. Both mating and dispersal behavior can be highly modified in social parasites, and many inquiline species are known to mate with their siblings inside the host nest instead of performing a mating flight, contributing to an inbred population structure and to a restricted biogeographic distribution of the species (Alpert and Akre 1973; Buschinger 1989; Bourke and Franks 1991; Aron et al. 1999; Buschinger and Linksvayer 2004; Trontti et al. 2005; Satoh and Ohkawara 2008; Rabeling and Bacci 2010; Heinze et al. 2015). Queens of *N. deceptrix* have reduced wings in comparison to the host and behavioral tests revealed the queens' inability to fly (Messer et al. 2016). *Nylanderia deyrupi* also has significantly smaller wings relative to the host (Fig. 8A), and the males of both *N. deceptrix* and *N. deyrupi* are brachypterous and apterous, respectively, suggesting that both species likely mate inside or close to the host nest. Interestingly, alate queens of *N. deyrupi* were collected in malaise traps. If the trap was not installed on top of the nest and *N. deyrupi* queens did not simply crawl into the trap, this observation suggests that alates may mate in the host nest but that queens are still capable of dispersing on the wing. In contrast, both queens and males of *N. parasitica* do not have significantly smaller wings when compared to the host (Fig. 8A, B) and the wider geographic distribution could be indicative of mating and/or dispersal flights occurring in *N. parasitica*. Direct observations of the mating behavior are missing for all three social parasite spe-

cies, however, and when sufficient samples become available, future studies need to test directly for population genetic signatures of inbreeding in *Nylanderia* social parasites.

Reduction of antennal segments. One trait of the inquiline syndrome that is unique to *N. parasitica* and absent from *N. deceptrix* and *N. deyrupi* is the reduction in the number of antennal segments from 13 to 12 in males. A reduction of antennal segments has been observed in some social parasite species of fungus-growing ants, such as *Pseudoatta argentina* and *Mycocepurus castrator* (Gallardo 1916; Rabeling and Bacci 2010). The reduction of antennal segments is potentially correlated with a reduced number of olfactory receptors, but this hypothesis remains to be tested.

Outlook

With currently three known social parasite species, the genus *Nylanderia* developed into an interesting study system for exploring the evolutionary history of social parasitism in a comparative context. In general, inquiline social parasites are of interest to evolutionary biology because of their departures from a free-living life history, the convergent morphological and behavioral evolution of traits associated with the socially parasitic life history, as well as their close phylogenetic relationships to their hosts. Previous studies revealed that some inquiline species evolved directly from their host species via sympatric speciation (Savolainen and Vepsäläinen 2003; Rabeling et al. 2014; Leppänen et al. 2015; Nettel-Hernanz et al. 2015) whereas other inquilines likely originated in allopatry (Agosti 1994; Sanetra and Buschinger 2000; Ward et al. 2015). In a forthcoming study, we will test whether *Nylanderia* inquilines evolved via the intra- or the interspecific route of social parasite evolution. In addition to inferring the evolutionary history, it is critical to study the behavior and natural history of *Nylanderia* inquilines to gain a more detailed understanding of their biology.

Acknowledgements

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RESEARCH ARTICLE

Notes on the genus *Trigonotoma* from China, with descriptions of two new species (Carabidae, Pterostichinae)

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Abstract

The genus *Trigonotoma* in China is studied, with descriptions of two new species, *T. digitata* **sp. nov.** and *T. constricta* **sp. nov.** One species is reported as new to China, *Trigonotoma indica* Brullé, 1834. Species relationships within Chinese *Trigonotoma* are briefly discussed mainly based on the endophallic characters.

Keywords

character evolution, endophallus, key, Trigonotomina

Introduction

Trigonotoma is a genus under the subtribe Trigonotomina (Carabidae: Pterostichini) which can be easily recognized by the very short and wide mentum tooth. A total of 51 *Trigonotoma* species has been recorded mainly from Oriental Region (Roux et al. 2016). However, only three species were distributed in China: *T. lewisii* Bates, 1873 widely distributed in east Asia and abundant, *T. dohrni* Chaudoir, 1852 widely distributed in south China but relatively rare, and *T. sinica* Dubault, Lassalle & Roux, 2011 only recorded in Yunnan Province and very rare (Bates 1873, Dubault et al. 2010, Chaudoir 1852, Dubault et al. 2011). Herein, two new species and a new record are proposed.

The taxonomic value of the everted endophallus of Carabidae has been recognized in recent decades, both for systematics and species identification (Shi and Liang 2015, Zhu et al. 2018). Thus, we studied the male endophallus of all available Chinese species (five of six known species, except *Trigonotoma sinica*) and briefly discuss possible relationships of some of the species.

The primary purposes of this paper are to describe two new species of *Trigonotoma*, provide a key for Chinese *Trigonotoma* species determinations, and describe and illustrate the endophallus of five Chinese *Trigonotoma* species (except for *T. sinica*) and discuss their relationships.

Materials and methods

This paper is based primarily on examination of specimens from China. The majority of specimens examined, including all types of new species, are deposited in the collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**IZAS**). The specimens examined or cited from other collections are indicated with abbreviations.

CCCC	Collection of Changchin Chen, Tianjin, China
MNHN	Muséum National d'Histoire Naturelle, Paris, France
SNU	Shanghai Normal University, Shanghai, China
ZSM	Zoologische Staatssammlungen, München, Germany

The body length (**BL**) was measured from apical margin of labrum to elytral apex; the body width (**BW**) was measured along elytral greatest width. The metepisternum length (**ML**) was measured along its outer margin; the basal width (**MW**) was measured along its oblique basal margin (Fig. 13). The pronotum basal width (**PBW**) was measured along its basal margin. For description of the endophallus, all lobes were named based on their homology inferences but not actual locations. The abbreviations used in endophallus are as follows: gonopore (**gp**), gonopore lobe (**gpl**), V-shaped setose area (**sa**), basal band (**bb**), chitinized piece (**cp**), basal lobe (**bl**), apical lobe (**al**), apical lobe-1 (**al-1**), apical lobe-2 (**al-2**), apical lobe-3 (**al-3**), left lobe (**ll**), left basal lobe (**lb**), left basal lobe-1 (**lb-1**), left basal lobe-2 (**lb-2**), left apical lobe (**la**), right lobe (**rl**). Other terms used and methods of measurement, preparation of figures, dissection, and endophallus everting procedures are mainly consistent with what we adopted in our previous work (Shi et al. 2013; Shi and Liang 2015).

Taxonomy

Genus *Trigonotoma* Dejean, 1828

Type species. *Trigonotoma viridicollis* Dejean, 1828 [= *Trigonotoma indica* Brullé 1834]

Diagnosis. Among the six genera (*Trigonotoma* Dejean, 1828, *Lesticus* Dejean, 1828, *Euryaptus* Bates, 1892, *Nesites* Andrews, 1931, *Pareuryaptus* Dubault, Lassalle & Roux, 2008, and *Leiolesticus* Roux, Lassalle & Dubault, 2016) of Trigonotomina, *Trigonotoma* can be distinguished from others in the subtribe by the following character combinations: first antennomere (scape) longer than the lengths of the 2nd, 3rd, and 4th antennomeres combined; apex of labrum emarginate, with six setae equidistantly placed; mentum notably shortened; parascutellar striae present; third elytral interval without setigerous pore; posterior margin of sternite VII with four setae in females. Detailed descriptions and distributions have recently been provided (Roux et al. 2016).

Key to Chinese species of *Trigonotoma*

1 Metepisternum short and wide, length less than or subequal to its basal width (ML/MW<1) (Fig. 13B) **2**
– Metepisternum long and narrow, length much greater than its basal width (ML/MW > 1.3) (Fig. 13A) **3**
2 Pronotum slightly narrowed to the base, very similar to that of *T. lewisii* (PW/PL = 1.27, PW/PBW = 1.55); pronotal basal foveal grooves well defined and separated (Figs 15, 17); male genitalia with the left margin of apical orifice strongly prominent and then deeply notched (Fig. 3) .....***T. digitata* sp. nov.**
– Pronotum strongly widened near middle and constricted to the base (PW/PL = 1.36, PW/PBW = 1.81); pronotal basal fovea with inner and outer grooves vaguely defined, partly fused (Figs 14, 16); male genitalia with the left margin of apical orifice gently sinuate near middle (Fig. 7) ......***T. constricta* sp. nov.**
3 Pronotum lateral margins strongly sinuate before posterior angles, posterior angles pointed (Fig. 18) .... ***T. indica* Brullé**
– Pronotum lateral margins not or only weakly sinuate before posterior angles, posterior angles rounded (Figs 19–21) **4**
4 Pronotum completely black, not metallic...
....***T. sinica* Dubault, Lassalle & Roux, 2010**
– Pronotum greenish to cupreous metallic **5**
5 Pronotum with dense and coarse punctures in the middle-basal area between basal fovea (Fig. 21); pronotum weakly narrowed to the base.........................
.... ***T. dohrni* Chaudoir, 1852**
– Pronotal base completely glabrous (Fig. 20), or with a few punctures restricted in the basal fovea area, the middle region between basal fovea completely glabrous (Fig. 19); pronotum distinctly narrowed to the base.......................
.... ***T. lewisii* Bates, 1873**

Trigonotoma digitata sp. nov.

http://zoobank.org/8B91DE0C-06A8-41CD-80DB-578B369A1E7B

Figures 1–4

Type locality. Guangdong: Xinfeng, Yunji Mountain (24.12N, 114.16E), altitude 1318 m.

Type material. *Holotype*: Male (IZAS), BL = 17.2 mm, board mounted, genitalia preserved in 100% ethanol in a microvial pinned under specimen, "China, Guangdong, Xinfeng, Yunji Mountain, pitfall trap, 24.115841N, 114.163535E"; "1318 m, 2017.V.20–25, Liu Y. Z. & Yu S. P. lgt., Institute of Zoology, CAS, Yunji Mountain, Xinfeng"; "HOLOTYPE ♂ *Trigonotoma digitata* sp. nov., des. ZHU & SHI 2019" [red label].

Diagnosis. Dorsal side bicolored, with strong metallic luster, pronotum cupreous green, elytra dark purple; pronotum slightly narrowed to the base; posterior angles completely rounded; pronotal base including the basal fovea completely glabrous; basal fovea with inner and outer grooves well defined; metepisternum short and wide, length subequal to its basal width; median lobe of aedeagus strongly lobed and notched on the left margin.

Comparison. The new species is different from all other known species of *Trigonotoma* by its distinct male genitalia (Fig. 3). At first glance, the new species is very similar to *T. lewisii* in external appearance, but these two species can be readily distinguished by the differences of metepisternum and male genitalia.

Description. BL = 17.2 mm, BW = 6.2 mm. Dorsal side bicolored with strong metallic luster: head and pronotum cupreous green, elytra purple; appendages dark, antennomeres 2–11, labial and maxillary palpi, apex of mouthparts and tarsomeres dark brown; ventral side black, without metallic luster. Head and pronotum with isodiametric microsculpture and minute punctures; elytra with transversal microsculpture.

Head with vertex smooth; frontal impressions deep and straight, longitudinally extending to the level of midpoint of eyes; labrum and clypeus both with anterior margins deeply emarginate; temporae straight, not swollen behind eyes; antennae reaching pronotum basal quarter.

Pronotum slightly transverse, PW/PL = 1.24, widest near anterior third; lateral margins curved in middle, and then gently narrowed to base, PW/PBW = 1.55; lateral margins straight in front of posterior angles, posterior angles rounded, not forming distinct angle; anterior margin straight, anterior angles widely rounded; posterior margin of nearly same width as anterior margin, gradually extended backward at lateral sides; disc completely glabrous, gently convex; median line fine but clearly defined, almost reaching posterior margin. Basal fovea deep and glabrous, without puncture or wrinkle; inner and outer grooves well defined, region between them deeply depressed, inner groove straight, slightly longer than curved outer groove.

Elytra oviform, EL/EW = 1.63, widest near posterior third; basal ridge complete, curved at fourth interval; humeral angles rounded, without teeth; intervals fairly convex, striae deeply incised, with coarse punctures; parascutellar striae short, apex almost conjunct to first stria; parascutellar pore present; third interval without setigerous pore; umbilical series on ninth interval composed of approximately 25 pores, sparse in middle.
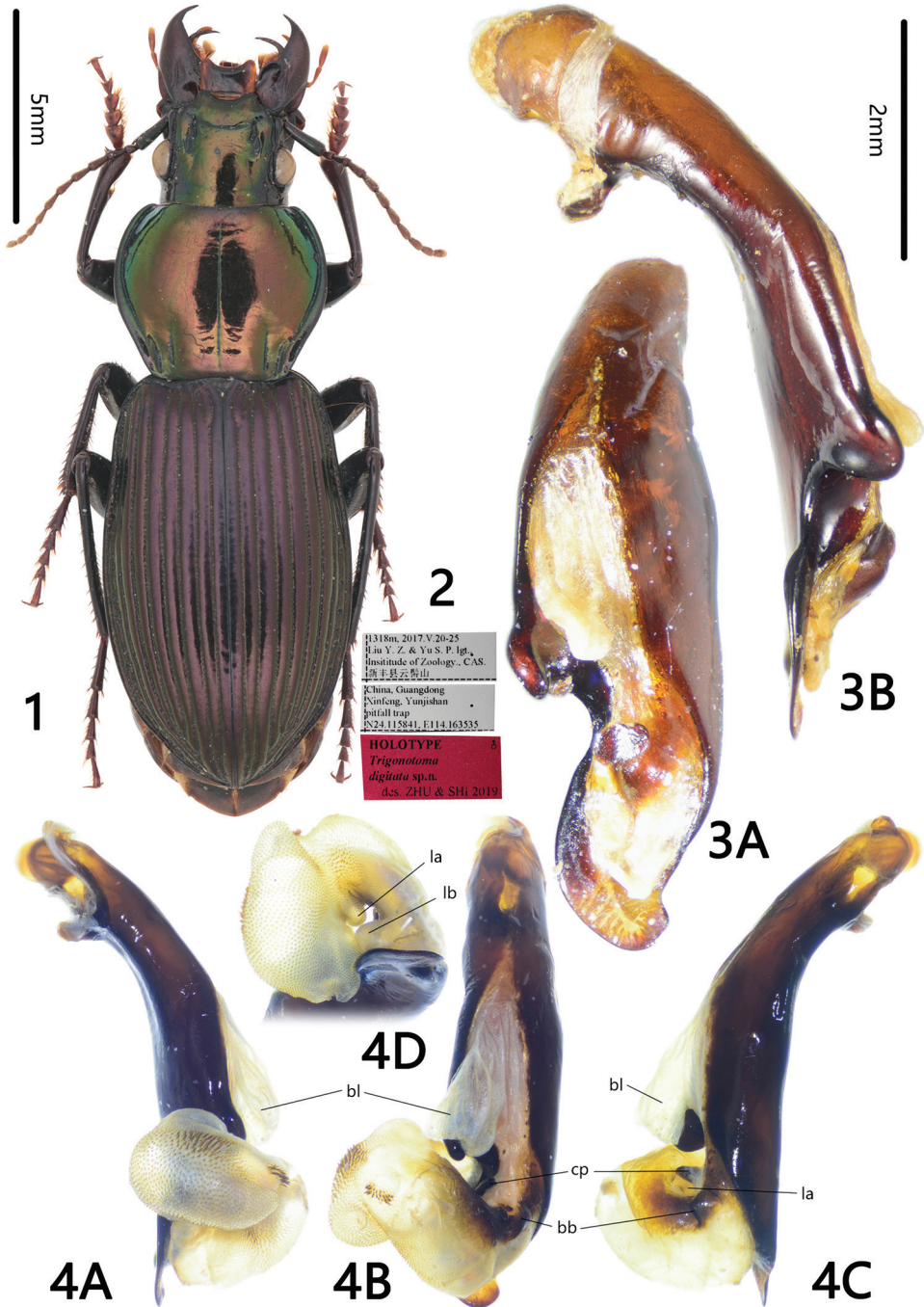
Figures 1–4. *Trigonotoma digitata* sp. nov. **1** Habitus of holotype (male, Guangdong, IZAS) **2** labels of holotype **3** median lobe of aedeagus (holotype) **A** dorsal view **B** left lateral view **4** endophallus (holotype) **A** left lateral view **B** dorsal view **C** right lateral view **D** apical view.

Ventral side: Propleuron and mesoepisternum with sparse and coarse punctures; metepisternum short and wide, ML/MW = 1.02, with sparse and coarse punctures; abdominal sternites glabrous on middle, with a few coarse punctures on lateral sides of sternites II and III, and shallow wrinkles on lateral sides of all sternites.

Legs: Metatarsomeres I and II strongly carinate on basal 3/4 of outer surface, distinctly carinate on basal half of mesotarsomere I and metatarsomere III; fifth tarsomeres of all legs with three or four pairs of spines ventrally.

Median lobe of male genitalia bent approx. 45° (the included angle between apical lamella and axes of basal portion of aedeagus). Apical orifice long and sinuate, constricted in middle, opened dorsally, and slightly turned to left. In dorsal view, right margin of aedeagus straight, and then sinuate before apical lamella; left margin with a digitiform lobe near midpoint of apical orifice, deeply notched anterior to lobe, and then widely arched reaching apex of apical lamella; apex of digitiform lobe rounded and bent to dorsal side; apical lamella short and wide, length approx. half its basal width; strongly bent to right, apex truncated, without tooth; dorsal surface without ridge.

Endophallus (Fig. 4) rotated to dorsal-left direction of aedeagus, major portion of endophallus on dorsal side of aedeagus; gpl folded so, invisible in Fig. 4; bb elongated, extended from apical orifice to middle part of endophallus; cp at left margin of apical orifice. Three distinct lobes recognized: bl moderately large, slightly prolonged, located at base of apical orifice, pointing to apical direction of aedeagus, membranous, without scales; lb small, rounded, located at base of endophallus and left side of apical orifice, pointing to left basal direction of aedeagus; la smaller than lb, rounded, located at left side of endophallus, with fine scales. Apex of endophallus large, elongate, with heavy spines on central and basal surfaces, and fine scales on other areas.

Distribution. Yunji Mountain, Xinfeng, Guangdong. Only known from the holotype.

Etymology. The specific epithet *digitata* is based on the Latin for finger and indicates the finger-shaped lobe on the aedeagus of the males. It is treated as an adjective in the nominative singular.

Trigonotoma constricta sp. nov.

http://zoobank.org/25E4489B-A3BF-4FCD-8F2F-C0E8A954F79C

Figures 5–8

Type locality. Hunan: Guidong, Bamian Shan Mt. (25.99N, 113.71E), altitude 1510 m.

Type material. ***Holotype:*** Male (IZAS), BL = 15.8 mm, board mounted, genitalia preserved in glycerin in a microvial pinned under specimen, "China, Hunan Guidong Co. Bamian Shan Mt., 25°59'33"N, 113°42'25"E, mixed forest, shrub, flower sifted & beating, ca. 1510m, 01.VI.2014, Peng, Shen, Yu & Yan"; "LX-5-1-1-8466"; "HOLOTYPE ♂ *Trigonotoma constricta* sp. nov., des. ZHU & SHI 2019" [red label].

Diagnosis. Dorsal side bicolored, pronotum metallic dark green, elytra dark purple; pronotum strongly narrowed to the base; posterior angles obtuse-rounded; pronotal base including the basal fovea completely glabrous; basal fovea with inner and outer

grooves vaguely defined, anterior half separated from each one, posterior half fused together; metepisternum short and wide, length subequal to its basal width.

Comparisons. This new species can be readily distinguished from all other *Trigonotoma* from China by the narrowly constricted pronotum base. *Trigonotoma concinna* from Java has the pronotum shape and basal fovea very similar to *T. constricta*, but differs by its larger size (19–21 mm), longer metepisternum, and longer apical lamella of the aedeagus.

Description. BL = 15.8 mm, BW = 5.9 mm. Dorsal side bicolored with strong metallic luster: head and pronotum dark green, elytra purple; appendages dark, antennomeres 2–11, labial and maxillary palpi, apex of mouthparts and tarsomeres dark brown; ventral side black, without metallic luster. Head and pronotum with isodiametric microsculpture and minute punctures; elytra with transversal microsculpture.

Head with vertex smooth; frontal impressions deep and straight, longitudinally extending to the level of midpoint of eyes; labrum and clypeus both with anterior margins deeply emarginate. Temporae straight, not swollen behind eyes; antennae reaching pronotum basal quarter.

Pronotum wide and round, PW/PL = 1.39, widest slightly before middle; lateral margins strongly widened and curved near middle, and then strongly constricted to base, PW/PBW = 1.81; lateral margins straight before posterior angles, posterior angles obtuse, forming indistinct angles; anterior margin straight, anterior angles widely rounded; posterior margin with width approximately equal to that of anterior margin, very slightly extended backward at lateral sides. Disc completely glabrous, gently convex; median line fine but clearly defined in middle, gradually shallowed, reaching neither posterior nor anterior margin; basal fovea deep and glabrous, without puncture or wrinkle; inner and outer grooves vaguely defined, partly fused together, region between them deeply depressed, so that basal fovea forms simple depressions.

Elytra oviform, EL/EW = 1.54, widest near posterior third; basal ridge complete, sinuate at inner half; humeral angles rounded, without tooth, intervals fairly convex; striae deeply incised, with fine punctures; parascutellar striae short, apex conjunct to first stria; parascutellar pore present; third interval without setigerous pore; umbilicate series on ninth interval composed of approximately 25 pores, sparse in middle.

*Ventral side***:** Propleuron glabrous, mesoepisternum with dense and coarse punctures; metepisternum short and wide, ML/MW = 0.99, with dense and coarse punctures; abdominal sternites glabrous on middle, with a few coarse punctures on lateral sides of sternites II and III, and shallow wrinkles on lateral sides of all sternites.

*Legs***:** Metatarsomeres I and II strongly carinate almost along their full length of outer surface, very shallowly carinate on basal half of mesotarsomere I and metatarsomere III; fifth tarsomeres of all legs with three or four pairs of spines ventrally.

Median lobe of male genitalia bent approximately 60° (the included angle between apical lamella and axes of basal portion of aedeagus). Apical orifice long and wide, reaching basal fourth of aedeagus, opened dorsally, slightly turned to left; right margin of apical orifice straight, left margin gently sinuate and notched near middle. In lateral view, aedeagus apex slightly bent downwards; ventral margin almost straight;
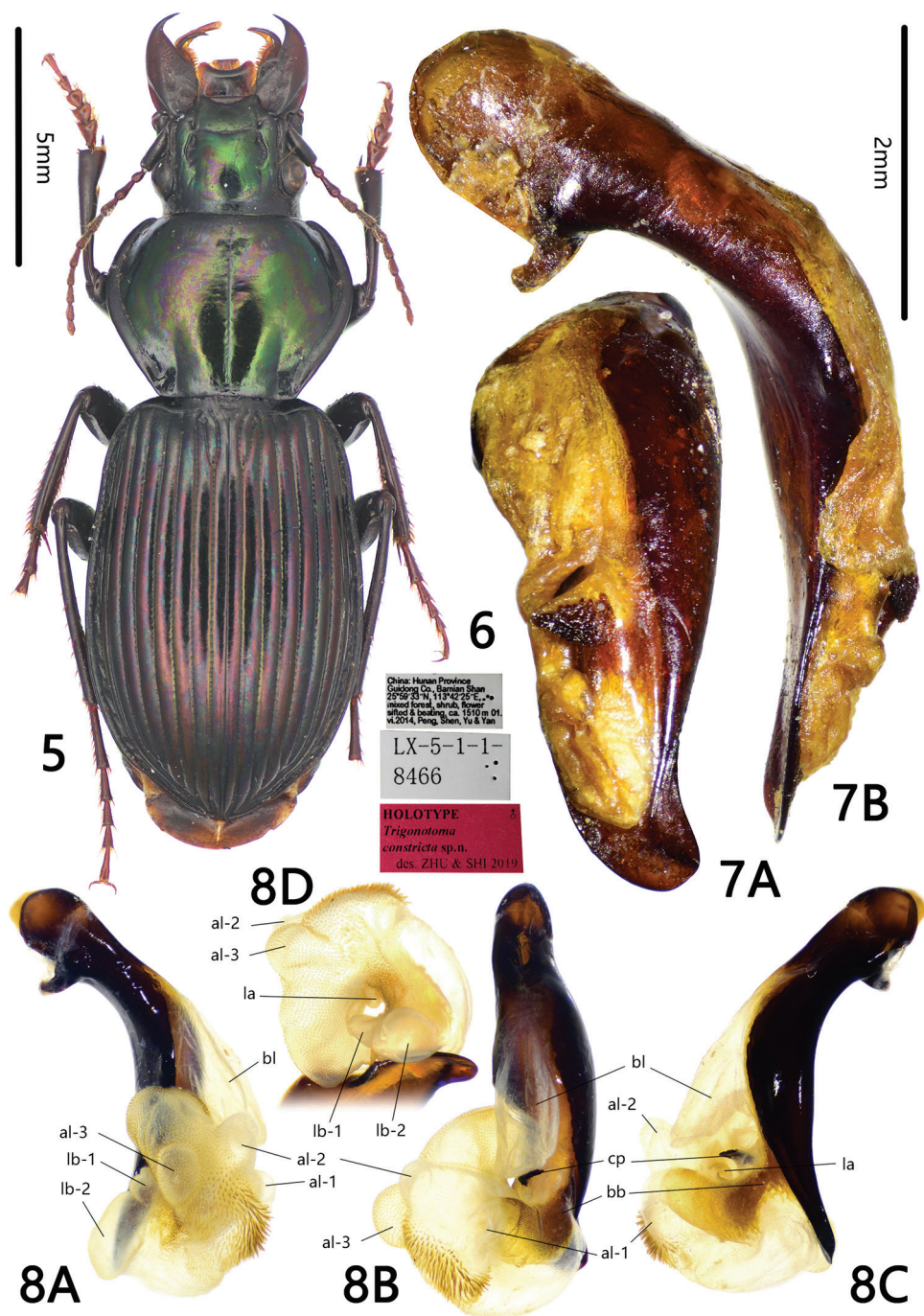
Figures 5–8. *Trigonotoma constricta* sp. nov. **5** Habitus of holotype (male, Hunan, IZAS) **6** labels of holotype **7** median lobe of aedeagus (holotype) **A** dorsal view **B** left lateral view **8** endophallus (holotype) **A** left lateral view **B** dorsal view **C** right lateral view **D** apical view.

apical lamella slightly thickened near base. In dorsal view, aedeagus apex broadly bent to right side; apical lamella length subequal to its basal width, with an indistinct oblique ridge, apex rounded-truncate, without tooth.

Endophallus (Fig. 8) rotated to dorsal-left direction of aedeagus, major portion of endophallus on dorsal side of aedeagus; gpl folded so, invisible in Fig. 8, bb short, not reaching middle part of endophallus; cp at left margin of apical orifice. Seven distinct lobes recognized: bl moderately large, slightly prolonged, located at base of apical orifice, pointing to apical direction of aedeagus, membranous, without scales; lb-1 small, rounded, located at base of endophallus and left side of apical orifice, pointing to left basal direction of aedeagus, without decorations; lb-2 larger than lb-1, elongate, located at right side of lb-1, pointing to left apical direction of aedeagus, without decoration; la smaller than lb-1, rounded, located at left side of endophallus, with fine scales; al-1 small, rounded, located at right basal side of endophallus, without decoration; al-2 slightly larger than al-1, rounded, located at right apical side of endophallus, decorated with very fine scales; al-3 with same size as al-2, rounded, located at left apical side of endophallus, decorated with fine scales. Apex of endophallus large, elongate, with a list of heavy spines on central surface, and fine scales on other area.

Distribution. Bamian Shan Mt., Guidong, Hunan. Only known from the holotype.

Etymology. The specific epithet *constricta* refers to the narrowly constricted base of the pronotum. It is treated as an adjective in the nominative singular.

Trigonotoma indica **Brullé, 1834, new record**
Figures 9–12

Brullé, 1834: 333 (Original: *Trigonotoma*, type in MNHN; type locality: Bengale); Chaudoir, 1868: 158; Bates, 1886: 145; Csiki, 1929: 517; Andrewes, 1930: 354; Andrewes, 1938: 138; Morvan, 1994: 328; Lorenz, 2005: 895; Dubault et al., 2007: 210; Kirschenhofer, 2007: 8; Dubault et al., 2008: 179; Roux et al., 2016: 122; Löbl I & Löbl D, 2017: 755.

viridicollis Dejean, 1828: 183, (Original: *Trigonotoma*; type in MNHN; type locality: India); Guérin-Méneville, 1829:44; Andrews, 1919: 148. Unavailable name, misidentification of *Omaseus viridicollis* Macleay, 1825. (Synonym)

baehri Kirschenhofer, 1997: 700, (Original: *Trigonotoma*; type in ZSM; type locality: C-Indien, MPR. Panna, Nat. Park). (Synonym)

Type locality. Bangladesh.

Material examined. 1 male (IZAS), "China, Tibet, Mêdog, Baibung Township, 780 m, 2011.VIII.10–13, Bi W. X."; 1 female (CCCC), "China, Tibet, Mêdog, Baibung Township, 700 m, 2011.VIII.09, YANG X. D. Leg. B11y2633, CCCC"; 1 female (IZAS), "Mêdog, light trap, 2016.VIII.5, Qiu T. F."; 18 males and 30 females (CCCC), "India, Andhra Pradesh Nellore District, Naidupet Mandal, Dwarakauram vili., 2010.IX.11–X.3, Chen C. C. Leg.".
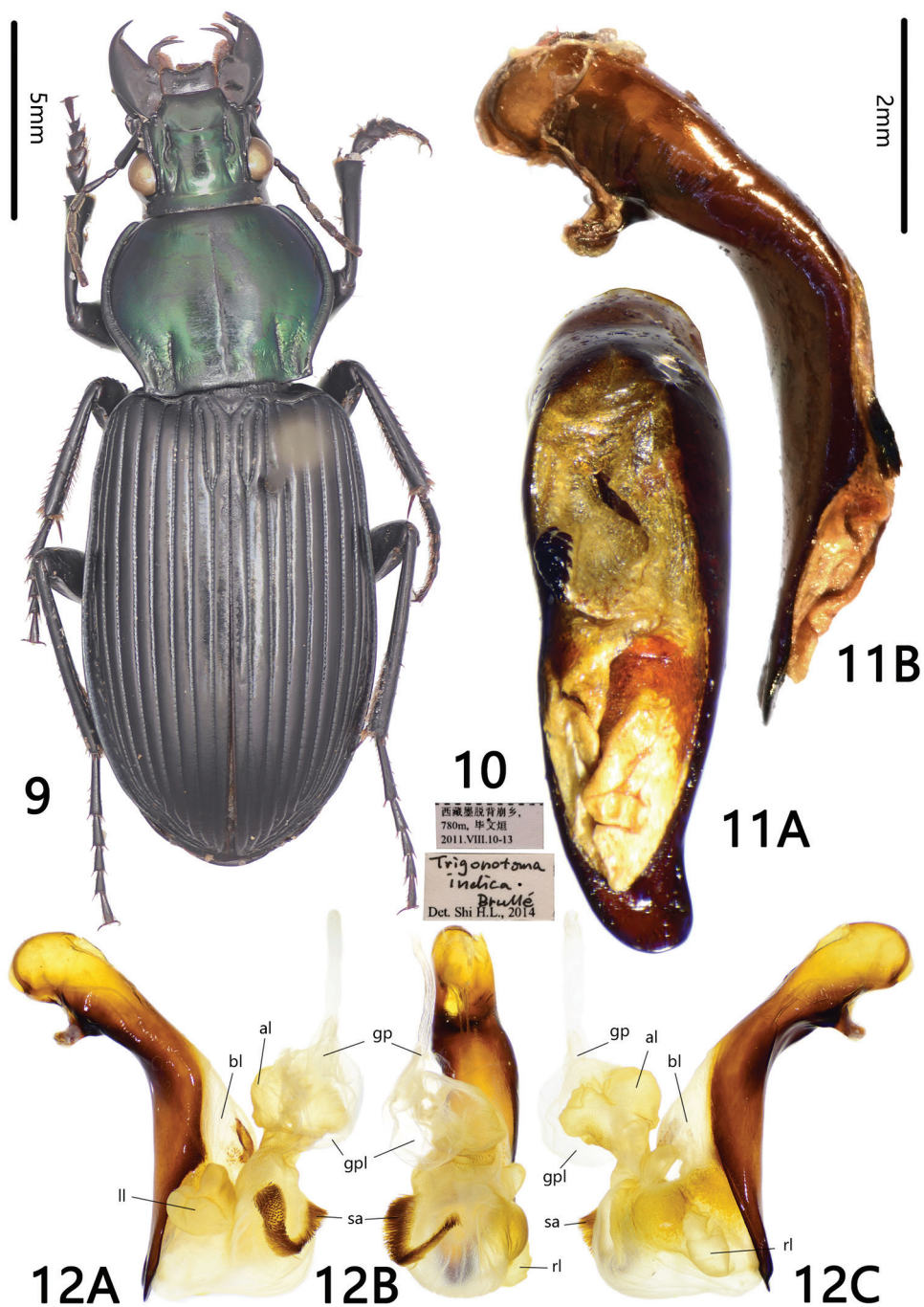
Figures 9–12. *Trigonotoma indica* Brullé, 1834. **9** Habitus (male, Xizang, IZAS) **10** labels **11** median lobe of aedeagus **A** dorsal view **B** left lateral view **12** endophallus **A** left lateral view **B** dorsal view **C** right lateral view.
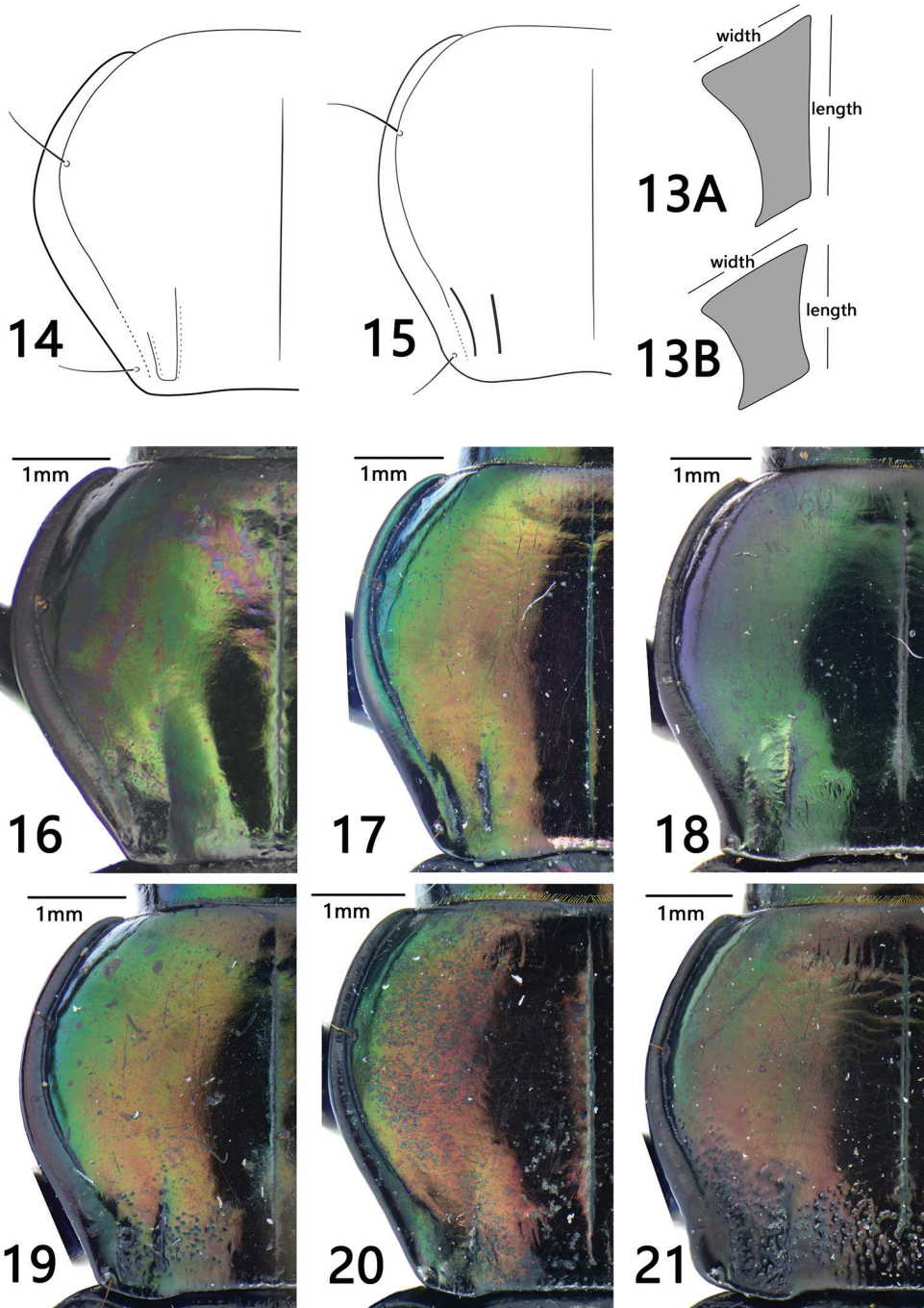
Figures 13–21. 13 Metaepisternum **A** *Trigonotoma lewisii* (long and narrow) **B** *T. constricta* (short and wide) **14–21** pronotum **14, 16** *T. constricta* **15, 17** *T. digitata* **18** *T. indica* **19, 20** *T. lewisii* **21** *T. dohrni*.

Diagnosis. BL = 20mm. Dorsal side bicolored, pronotum with metallic luster, purple, green, blue or nearly black, elytra black with faint metallic reflections; pronotum lateral margins strongly sinuate in front of posterior angles; posterior angles sharp and base rectangular; basal fovea more or less punctate and rugose; metepisternum long and narrow; apical lamella of aedeagus with rounded apex, shallowly notched or not. *Trigonotoma indica* can be readily distinguished from all other Chinese species by the pronotum lateral margins that are strongly sinuate near base.

Supplementary descriptions on endophallus. Endophallus (Fig. 12) bent to dorsal direction of aedeagus, major portion of endophallus on dorsal side of aedeagus; gp located at approx middle of aedeagus, oriented to aedeagal base; gpl large, rounded, membranous, bb absent; cp absent. Four distinct lobes recognized: bl moderately large, slightly prolonged, located at base of apical orifice, pointing to apical direction of aedeagus, with a few scales on left side; ll moderately large, divided into several sublobes, located at left side of endophallus, with fine scales; rl smaller than ll, rounded, located at right side of endophallus, with fine scales; al large, divided into several sublobes, located at apex of endophallus, connected with base of endophallus through a narrow area, forming a dumbbell-shape, with fine scales. Middle of endophallus large, rounded, with a V-shaped sa on left middle and fine scales on apex.

Distribution. China (Tibet: Mêdog), India, Bangladesh, Sri Lanka, and Pakistan. Another subspecies, *T. indica nepalensis*, is distributed in Nepal.

Remarks. It is expected this species would be found to be widely distributed in and around China. Identification is based on the comparison of the image of holotype (Roux et al. 2016) and specimens from Andhra Prad., India. Compared with the specimens from India, *T. indica* from Mêdog is slightly larger and more vividly green on its pronotum.

Discussion

Before the present study, three *Trigonotoma* species were recorded from China. Here, we add three more species bringing the total number of Chinese *Trigonotoma* to six. Preliminary conclusions on species relationships within Chinese *Trigonotoma*, mainly based on the endophallic characters, are presented below.

The endophallus characters of *T. constricta* and *T. digitata* are very similar, sharing the same bb, cp, bl, la and dorsal-left rotation. Their main differences are that in *T. digitata*, lb is divided into lb-1 and lb-2 and three apical lobes (al-1, al-2 and al-3) appear on apex of endophallus, which makes it more complex than in *T. constricta*. In addition to characteristics of the endophallus, the short metepisternum is another important shared character state. As we discussed in the previous paper (Zhu et al. 2018), the shape of metepisternum has important taxonomic value in *Lesticus*. The shortened metepisternum is apomorphic in *Trigonotoma*, similar to what is found in *Lesticus* and several groups of Carabidae. The two species described here are the first known with short metepisternum from China. Among all *Trigonotoma*, only five other species are known to have this character: *Trigonotoma morvani* Deuve & Lassalle, *T. himalchuliensis* Lassalle
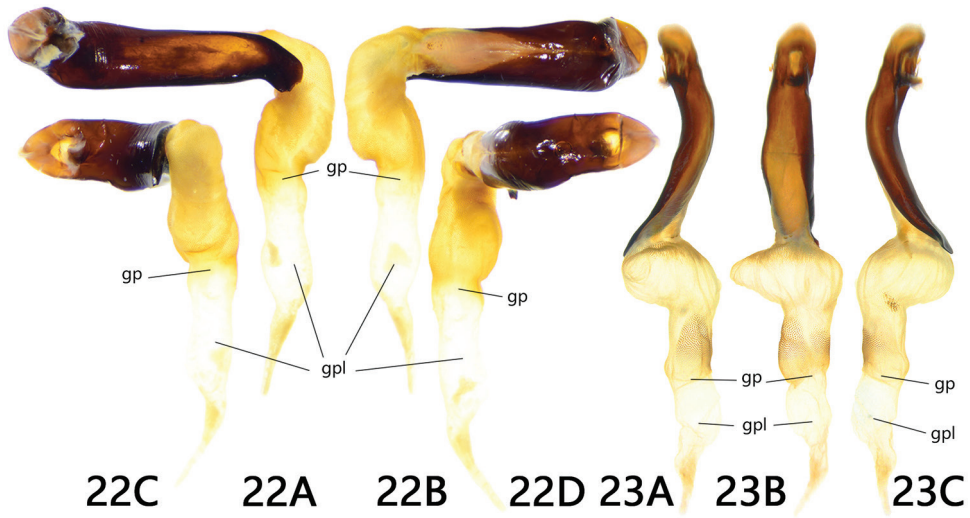
Figures 22, 23. Endophallus **22** *Trigonotoma dohrni* **A** ventral view **B** dorsal view **C** apical view **D** basal view **23** *T. lewisii* **A** left lateral view **B** dorsal view **C** right lateral view.

(Nepal), *T. cylindriceps* Straneo (India), *T. igneicollis* Bates (Myanmar), and *T. buehleri* Straneo (Indonesia, Sumba). The two newly described Chinese species are hypothesized to be closely related, possibly sister species, based on the character of metepisternum, the shared dorsal-left curled endophallus, and the adjacent distributions.

Two previously described species were also studied. The endophallus of *T. lewisii* and *T. dohrni* show extensive similarity but are quite different from *T. digitata* and *T. constricta*. They have a shared character of a prolonged, straight, and nearly glabrous endophallus without any lobe, scale, setose, band, or chitinized piece. Moreover, bl, cp, and bb are also absent. These two species are different from each other in the orientation of endophallus: *T. lewisii* extending to genital apex, slightly deflected to dorsum, gonopore oriented to aedeagal apex (Fig. 23), while *T. dohrni* markedly deflexed to the right, forming a right angle with aedeagus, and gonopore oriented to the right side of aedeagus (Fig. 22). As to the external characters, they have completely different pronotal form but similar long metapisternum. Additionally, they are both widely distributed in south China, Myanmar, and Vietnam, while *T. lewisii* is also distributed in north China, Korea, and Japan (Fig. 24). In conclusion, a close relationship of these two species is possible.

The endophallus of *T. sinica* has not been examined.

Trigonotoma indica is different from the species discussed above in terms of endophallus characters, external characters, and distribution. The endophallus of *T. indica* is bent in the dorsal direction and the gonopore is oriented toward the aedeagal base. In addition, cp and bb are absent, but a V-shaped sa appears on the left middle of endophallus. And the posterior angle is pointed and forms a right angle in *T. indica*. In all other Chinese *Trigonotoma*, however their pronotum lateral margin differs, it is not pointed. Outside of the Chinese fauna, there are five other species with pointed
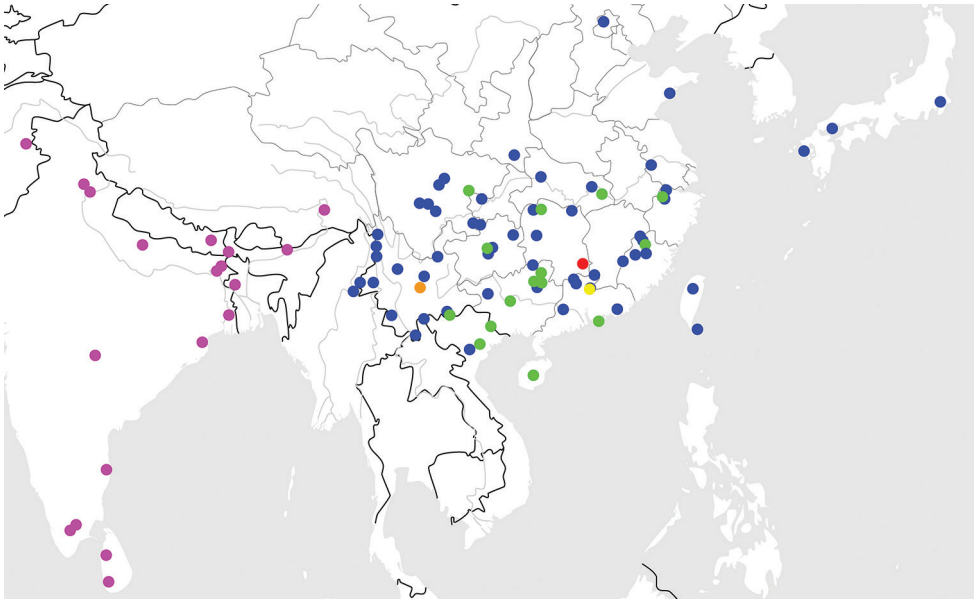
Figure 24. Distribution map for *Trigonotoma* from China: *T. constricta* sp. nov. (red); *T. digitata* sp. nov. (yellow); *T. sinica* Dubault, Lassalle & Roux (orange), the precise locality was not mentioned in the original literature; *T. dohrni* Chaudoir (green); *T. lewisii* Bates (blue); *T. indica* Brullé, 1834 (purple).

posterior angles: *T. oberthuri* Tschitscherine, *T. tenebrosa* Dubault et al., *T. cylindriceps* Straneo, *T. morvani* Deuve & Lassalle, and *T. himalchuliensis* Lassalle, all from Indian fauna. Additionally, the endophallus of the first two are bent in a dorsal direction and the gonopore is oriented towards the aedeagal base (Roux et al. 2016), the same as *T. indica*. Finally, considering the different distribution patterns and morphological characters, *T. indica* could be related to the above Indian species and distant from other four Chinese species.

Acknowledgements

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CHECKLIST

Commented checklist of European Gelechiidae (Lepidoptera)

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Abstract

The checklist of European Gelechiidae covers 865 species, belonging to 109 genera, with three species records which require confirmation. Further, it is the first checklist to include a complete coverage of proved synonyms of species and at generic level. The following taxonomic changes are introduced: *Pseudosophronia constanti* (Nel, 1998) **syn. nov.** of *Pseudosophronia exustellus* (Zeller, 1847), *Metzneria expositoi* Vives, 2001 **syn. nov.** of *Metzneria aestivella* (Zeller, 1839); *Sophronia ascalis* Gozmány, 1951 **syn. nov.** of *Sophronia grandii* Hering, 1933, *Aproaerema incognitana* (Gozmány, 1957) **comb. nov.**, *Aproaerema cinctelloides* (Nel & Varenne, 2012) **comb. nov.**, *Aproaerema azosterella* (Herrich-Schäffer, 1854) **comb. nov.**, *Aproaerema montanata* (Gozmány, 1957) **comb. nov.**, *Aproaerema cincticulella* (Bruand, 1851) **comb. nov.**, *Aproaerema buvati* (Nel, 1995) **comb. nov.**, *Aproaerema linella* (Chrétien, 1904) **comb. nov.**, *Aproaerema captivella* (Herrich-Schäffer, 1854) **comb. nov.**, *Aproaerema semicostella* (Staudinger, 1871) **comb. nov.**, *Aproaerema steppicola* (Junnilainen, 2010) **comb. nov.**, *Aproaerema cottienella* (Nel, 2012) **comb. nov.**, *Ptocheuusa cinerella* (Chrétien, 1908) **comb. nov.**, *Pragmatodes melagonella* (Constant, 1895) **comb. nov.**, *Pragmatodes albagonella* (Varenne & Nel, 2010) **comb. nov.**, *Pragmatodes parvulata* (Gozmány, 1953) **comb. nov.**, *Oxypteryx nigromaculella* (Millière, 1872) **comb. nov.**, *Oxypteryx wilkella* (Linnaeus, 1758) **comb. nov.**, *Oxypteryx ochricapilla* (Rebel, 1903) **comb. nov.**, *Oxypteryx superbella* (Zeller, 1839) **comb. nov.**, *Oxypteryx mirusella* (Huemer & Karsholt, 2013) **comb. nov.**, *Oxypteryx baldizzonei* (Karsholt & Huemer, 2013) **comb. nov.**, *Oxypteryx occidentella* (Huemer & Karsholt, 2011) **comb. nov.**, *Oxypteryx libertinella* (Zeller, 1872) **comb. nov.**, *Oxypteryx gemerensis* (Elsner, 2013) **comb. nov.**, *Oxypteryx deserta* (Piskunov, 1990) **comb. nov.**, *Oxypteryx unicolorella* (Duponchel, 1843) **comb. nov.**, *Oxypteryx nigritella* (Zeller, 1847) **comb. nov.**, *Oxypteryx plumbella* (Heinemann, 1870) **comb. nov.**, *Oxypteryx isostacta* (Meyrick, 1926) **comb. nov.**, *Oxypteryx helotella* (Staudinger, 1859) **comb. nov.**, *Oxypteryx parahelotella* (Nel, 1995) **comb. nov.**, *Oxypteryx graecatella* (Šumpich & Skyva, 2012) **comb. nov.**; *Aproaerema genistae* (Walsingham, 1908) **comb. rev.**, *Aproaerema thaumalea* (Walsingham, 1905) **comb. rev.**;

Dichomeris neatodes Meyrick, 1923 **sp. rev.**; *Caryocolum horoscopa* (Meyrick, 1926) **stat. rev.**; *Ivanauskiella occitanica* (Nel & Varenne, 2013) **sp. rev.**; *Apodia martinii* Petry, 1911 **sp. rev.**; *Caulastrocecis cryptoxena* (Gozmány, 1952) **sp. rev.** Following Article 23.9.2 ICZN we propose *Caryocolum blandella* (Douglas, 1852) (*Gelechia*) **nom. protectum** and *Caryocolum signatella* (Eversmann, 1844) (*Lita*) **nom. oblitum.**

Introduction

Lepidoptera, butterflies and moths, are among the best-known insects, and due to a long tradition of studying Lepidoptera in Europe our knowledge of European Lepidoptera is more comprehensive compared to other parts of the world. Even though Lepidoptera is a well-defined group they exhibit a huge diversity in size, colour and wing markings. Whereas everybody can recognize a butterfly the vast majority of Lepidoptera are small and often dull coloured insects. One such group is the family Gelechiidae. They have for a long time been rather neglected by most lepidopterists mainly due to their external similarity and lack of resources for their identification. Over the last couple of decades, the latter problem has partly been addressed, e.g., Elsner et al. (1999), Huemer and Karsholt (1999, 2010), and at the same time there has been an increasing research interest in the Gelechiidae, resulting in a number of smaller and larger taxonomic reviews and faunistic publications (see reference list) dealing with these moths. However, what was becoming increasingly a hindrance for ongoing research was the lack of an updated checklist of European Gelechiidae. In particular, when planning an extensive DNA barcoding project for the family (Huemer et al. 2020), this deficit became obvious and therefore the authors decided to compile such a checklist for this and future requirements.

A checklist is the most basic taxonomic work on a group of organisms. It can be alphabetical or systematic, viz. trying to reflect the current knowledge of the relationship of the included taxa. This checklist is in systematic order, and it moreover includes synonyms and annotations. Its aim is to present an updated overview of the Gelechiidae known from Europe. This is highly appropriate as nearly a quarter of the currently known species have been described since 1990 (Huemer et al. 2020).

This checklist of European Gelechiidae is the first one to include all known synonyms of genera and species of Europaean Gelechiidae. It is mainly based on data published in Fauna Europaea (Karsholt 2004–2019) but supplemented with numerous published and unpublished additions and corrections from the last few years. It covers all currently accepted species known from the European fauna and their synonyms. Subspecies are not given separate entries, but listed among synonyms, though marked as subspecies. Subgenera are listed among generic synonyms. The considerable number of likely undescribed species (Huemer et al. 2020) are not included in the list.

Taxonomically critical genera and species, especially possible cases of cryptic diversity (Fig. 1) manifested by divergent DNA barcodes, are commented on in detail (see also Huemer et al. 2020).

Figure 1. Alpine species of *Sattleria* are a striking example of long underestimated species diversity (photograph Michel Billard).

Materials and methods

Geographic restriction

For the purpose of the present checklist we define Europe in a broad sense, which includes the Ural Mountains, Russian parts of the Caucasus, the 'European' part of Kazakhstan, the Mediterranean islands and the Macaronesian Islands (except Cape Verde) (Fig. 2).

The inclusion of the Russian parts of the Caucasus only added four species to the list (*Acompsia caucasella* Huemer & Karsholt, *Neofriseria caucasicella* Sattler, *Chionodes caucasiella* Huemer & Sattler and *Scrobipalpa caucasica* (Povolný)), which is surprising. One would expect a richer gelechiid fauna to occur in this vast and diverse mountain system. However, most likely the species inventory is simply underestimated as only few lepidopterists have done field research in this area so far.

Content and structure of the checklist

The checklist is restricted to described nominal taxa. Potentially undescribed species (Huemer et al. 2020) are not included. Species introduced from other parts of the World are only included if they are known to have been naturalized within the area described above. Doubtful, though possible, records of occurrence are considered in the checklist

and marked with an asterisk *, whereas confirmed incorrect records and doubtful species (*taxa incertae sedis*) are not listed. Names applied to misidentified taxa are listed only in cases where the incorrect taxonomy has been widely used or where the misidentification can easily cause misunderstandings. These are marked with *auct.* (= of authors).

Systematic arrangement

The higher classification follows the molecular study of Karsholt et al. (2013), whereas the listed order of genera and species is largely according to published revisions and data from Huemer et al. (2020).

Synonymy

Although our knowledge of European Gelechiidae has increased much over the last years, there are still available species-group names in the family which have not yet been associated with known species. Very few of these are likely to represent additional taxa, whereas most cases will be synonyms. Furthermore, several of the published synonyms need taxonomic re-assessment. We have not made special efforts to search for type specimens of such taxa for the purpose of the present checklist, and they should be considered in connection with taxonomic revisions within the Gelechiidae.

Gender agreement

Many species-group names of European Gelechiidae have been combined in different genera since they were first made available. Following article 31.2 of the International Code of Zoological Nomenclature (ICZN 1999) these names require gender agreement between specific and generic names. However, we follow the widely accepted proposals by Sommerer (2002) in Lepidoptera and keep the original spelling of species names to avoid unnecessary instability (van Nieukerken et al. 2019).

Molecular species delimitation

DNA barcodes have been sequenced for a significant number of the species included in the inventory (741 nominal species with sequences > 500 bp). These supported the compilation of the checklist and helped identify and fix yet unpublished synonyms and the systematic position of some species. Details to species and specimens are available on BOLD (Ratnasingham 2018) in the public dataset "Lepidoptera (Gelechiidae) of Europe" under the DOI: https://doi.org/10.5883/DS-GELECHEU (see also Huemer et al 2020).

We tested the congruence of morphologically based species determinations and COI sequence data with the Barcode Index Number (BIN), a methodology recently
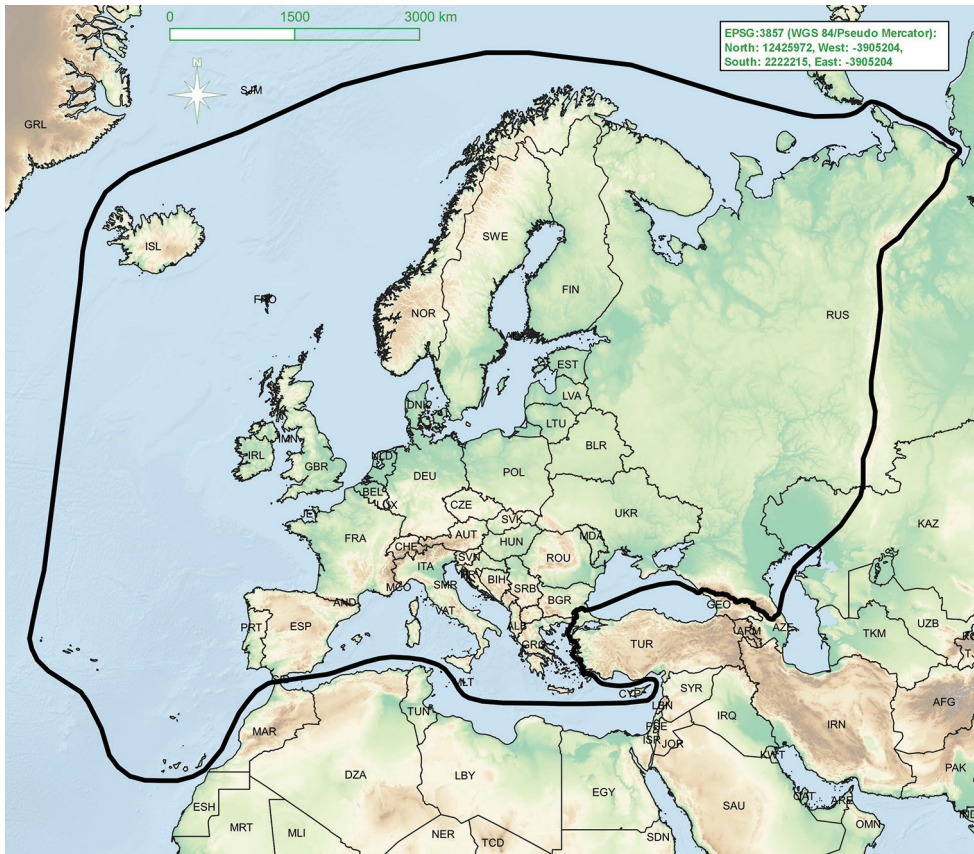
Figure 2. Geographical boundaries of research area. World boundaries: https://www.arcgis.com/; SRTM-Data: https://dds.cr.usgs.gov/srtm/version2_1/SRTM3/.

proposed by Ratnasingham and Hebert (2013). This system clusters sequences into Operational Taxonomic Units (OTUs) regardless of their previous taxonomic assignment. It is based on a two-stage algorithm that groups the sequences in a cluster and automatically assigns new sequences. All high-quality sequences > 500 bp are recorded independently of the project origin and assigned to a BIN. Though BINs reflect classical Linnean taxonomy to a high level they were not used uncontested (Huemer et al 2020). We found 114 morphologically delimited species with multiple BINs that are potential cases of cryptic diversity, particularly cases with BIN distances > 3%, and these are therefore discussed in the comments. However, there is clear evidence that no species delimiting threshold values exist in Lepidoptera (Kekkonen et al. 2015) and therefore all cases of barcode divergence require further and integrative analysis in the future. Such work was largely outside the scope of this paper which principally followed current taxonomy and only exceptionally considered obvious taxonomic issues. An in-depth taxonomical analysis will also be necessary for 65 clusters with a unique BIN which remained unidentified to species level from morphology and which are not considered in the checklist itself, and for 55 cases of BIN-sharing (see also Huemer et al. (2020)).

Table 1. Number of described species per tribe/subfamily.

Higher taxa	Species no.
Gelechiidae Stainton, 1854	**865**
Anacampsinae Bruand d'Uzelle, 1851	**89**
Anacampsini Bruand d'Uzelle, 1851	67
Chelariini Le Marchand, 1947	22
Dichomeridinae Hampson, 1918	**47**
Apatetrinae Le Marchand, 1947	**29**
Pexicopiini Hodges, 1986	6
Apatetrini Le Marchand, 1947	23
Thiotrichinae Karsholt, Mutanen, Lee & Kaila, 2013	**5**
Anomologinae Meyrick, 1926	**253**
Gelechiinae Stainton, 1854	**445**
Gelechiini Stainton, 1854	132
Gnorimoschemini Povolný, 1964	240
Litini Bruand d'Uzelle 1859	73

Results

Overview

The checklist covers 865 nominal species of European Gelechiidae belonging to 109 genera, including 3 species with doubtful records (*). The majority belong to Gelechiinae (445 spp.), followed by Anomologinae (253 spp.), Anacampsinae (89 spp.), Dichomeridinae (47 spp.), Apatetrinae (29 spp.), and Thiotrichinae (5 spp.) (Table 1).

Taxon excluded from the Gelechiidae

A single species originally described in the Gelechiidae is excluded from the family, viz. *Brachmia infuscatella* Rebel, 1940, and is transferred to Autostichidae without generic assignation.

Checklist

Numbers [1] – [202] refer to comments; * refers to doubtful records for the European fauna.

Gelechiidae Stainton, 1854
Anacampsinae Bruand d'Uzelle, 1851 [1]
　　Stomopteryginae Heslop, 1938, unavailable
Anacampsini Bruand d'Uzelle, 1851

***Stomopteryx* Heinemann, 1870 [2]**
　　Inotica Meyrick, 1913

    Acraeologa Meyrick, 1921
    Kahelia Turati, 1922, unavailable
Stomopteryx detersella (Zeller, 1847)
    egenella (Herrich-Schäffer, 1851), unavailable
    palermitella (La Harpe, 1860)
    tenuisignella Turati, 1924
    obliterella Turati, 1924, unavailable
Stomopteryx bolschewickiella (Caradja, 1920)
Stomopteryx nugatricella Rebel, 1893 **[3]**
Stomopteryx mongolica Piskunov, 1975 **[3]**
Stomopteryx lineolella (Eversmann, 1844) **[3]**
Stomopteryx basalis (Staudinger, 1876)
    oxychalca (Meyrick, 1937)
Stomopteryx deverrae (Walsingham, 1905) **[4]**
Stomopteryx flavoclavella Zerny, 1935 **[5]**
Stomopteryx remissella (Zeller, 1847) **[6]**
    vetustella (Herrich-Schäffer, 1854)
    tripunctigerella (Bruand d'Uzelle, 1859)
    submissella (Frey, 1880), homonym
    rufobasella (Rebel, 1916)
    yunusemrei Koçak, 1986
Stomopteryx spathulella Nel, Varenne & Labonne, 2019 **[6]**
Stomopteryx orthogonella (Staudinger, 1871)
Stomopteryx flavipalpella Jäckh, 1959 **[7]**
Stomopteryx hungaricella Gozmány, 1957
Stomopteryx lusitaniella Corley & Karsholt, 2014
Stomoptery jeppeseni Karsholt & Šumpich, 2018
Stomopteryx alpinella Nel & Varenne, 2016
Stomopteryx schizogynae (Walsingham, 1908)

***Aproaerema* Durrant, 1897 [8]**
    Harpagus Stephens, 1834, homonym
    Untomia Busck, 1906
    Schuetzeia Spuler, 1910
    Syncopacma Meyrick, 1925
    Lixodessa Gozmány, 1957
Aproaerema patruella (Mann, 1857)
    fulvistillella (Rebel, 1891)
Aproaerema coronillella (Treitschke, 1833)
    fournieri (Nel, 1998)
Aproaerema incognitana (Gozmány, 1957) **comb. nov. [8]**
Aproaerema sangiella (Stainton, 1863)
Aproaerema cinctella (Clerck, 1759) **[9]**

    vorticella (Scopoli, 1763)
    ligulella ([Denis & Schiffermüller], 1775)
    vittata (Fourcroy & Geoffroy, 1785)
    vittatella (Villers, 1789)
    albistrigella (Stephens, 1834)
    ussuriella (Caradja, 1920)
    finlandica (Gozmány, 1957)
Aproaerema cinctelloides (Nel & Varenne, 2012) **comb. nov. [8]**
Aproaerema larseniella (Gozmány, 1957)
    ligulella auct.
Aproaerema wormiella (Wolff, 1958) **[8]**
    parawormiella (Nel & Varenne, 2016)
Aproaerema azosterella (Herrich-Schäffer, 1854) **comb. nov. [8]**
Aproaerema ochrofasciella (Toll, 1936)
Aproaerema taeniolella (Zeller, 1839)
    sircomella (Stainton, 1854)
Aproaerema montanata (Gozmány, 1957) **comb. nov. [8]**
Aproaerema albifrontella (Heinemann, 1870)
    ignobilella (Heinemann, 1870)
Aproaerema cincticulella (Bruand, 1851) **comb. nov.**
Aproaerema vinella Bankes, 1898
    fasciata Bankes, 1898, unavailable
    biformella Schütze, 1902
Aproaerema buvati (Nel, 1995) **comb. nov. [8]**
Aproaerema linella (Chrétien, 1904) **comb. nov. [8, 10]**
    schoenmanni (Gozmány, 1957)
Aproaerema albipalpella (Herrich-Schäffer, 1854)
    leucopalpella (Herrich-Schäffer, 1854), unavailable
    ruptella (Constant, 1865)
Aproaerema suecicella (Wolff, 1958) **[11]**
Aproaerema captivella (Herrich-Schäffer, 1854) **comb. nov. [8]**
    sarothamnella (Zeller, 1868)
Aproaerema polychromella (Rebel, 1902)
    argyrolobiella Caradja, 1920, unavailable
    faceta (Meyrick, 1914)
Aproaerema karvoneni (Hackman, 1950) **[12]**
Aproaerema semicostella (Staudinger, 1871) **comb. nov. [8]**
    albicapitella (Bidzilya, 1996)
Aproaerema steppicolella (Junnilainen, 2010) **comb. nov. [8]**
Aproaerema cottiennella (Nel, 2012) **comb. nov. [8]**
Aproaerema genistae (Walsingham, 1908) **comb. rev. [8]**
Aproaerema thaumalea (Walsingham, 1905) **comb. rev. [8]**
Aproaerema anthyllidella (Hübner, 1813) **[13]**

    caliginosella (Duponchel, 1843)
    elachistella (Stainton, 1859), subspecies
    psoralella (Millière, 1865)
    lachtensis (Erschoff, 1877)
    sparsiciliella (Barrett, 1891)
    infestella (Rebel, 1896)
    natrixella (Weber, 1945)
    brundini (Benander, 1945)
    alfalfella Amsel, 1958
    aureliana Căpuşe, 1964
Aproaerema lerauti Vives, 2001
Aproaerema mercedella Walsingham, 1908

Iwaruna Gozmány, 1957 [14]
Iwaruna heringi Gozmány, 1957
Iwaruna biguttella (Duponchel, 1843)
Iwaruna klimeschi Wolff, 1958
Iwaruna robineaui Nel, 2008

Anacampsis Curtis, 1827
    Tachyptilia Heinemann, 1870
    Agriastis Meyrick, 1914
Anacampsis populella (Clerck, 1759) **[15]**
    tremella ([Denis & Schiffermüller], 1775)
    boeberana (Fabricius, 1787)
    populi (Haworth, 1828), emendation
    laticinctella Stephens, 1834
    tremulella Duponchel, 1839
    atra (Strand, 1901), unavailable
    lugens (Caradja, 1920)
    sachalinensis (Matsumura, 1931)
    fuscatella (Bentinck, 1934)
    ambronella (Meder, 1934)
    ceballosi Agenjo, 1959
Anacampsis blattariella (Hübner, 1796) **[15]**
    thapsiella (Hübner, 1796)
    blattariae (Haworth, 1828), emendation
    atragriseella Bruand d'Uzelle, 1851
    betulinella Vári, 1941
Anacampsis timidella (Wocke, 1887)
    quercella (Chrétien, 1907)
    disquei (Meess, 1907)
    suberiella Caradja, 1920

Anacampsis scintillella (Fischer v. Röslerstamm, 1841) **[16]**
    brunneella Herrich-Schäffer, 1854
    contuberniella (Staudinger, 1859)
Anacampsis temerella (Lienig & Zeller, 1846)
    pernigrella (Douglas, 1850)
Anacampsis trifoliella (Constant, 1890)
Anacampsis fuscella (Eversmann, 1844)
Anacampsis hirsutella (Constant, 1885)
Anacampsis obscurella ([Denis & Schiffermüller], 1775) **[17]**
    subsequella (Hübner, 1796)
Anacampsis malella Amsel, 1959

***Mesophleps* Hübner, 1825 [18]**
    Brachyacma Meyrick, 1886
    Lathontogenus Walsingham, 1897
    Paraspistes Meyrick, 1905
    Chretienia Spuler, 1910
    Lipatia Busck, 1910
    Stiphrostola Meyrick, 1923
    Crossobela Meyrick, 1923
    Xerometra Meyrick, 1925
    Gnosimacha Meyrick, 1927
    Bucolarcha Meyrick, 1929
    Uncustriodonta Agenjo, 1952
Mesophleps corsicella (Herrich-Schäffer, 1856)
    lala Agenjo, 1961
Mesophleps silacella (Hübner, 1796)
    pyropella auct.
    luteella (Hübner, 1896), unavailable
    silacea (Haworth, 1828), emendation
    apicellus Caradja, 1920
    calaritanus Amsel, 1939
Mesophleps oxycedrella (Millière, 1871)
Mesophleps trinotella Herrich-Schäffer, 1856
    aurantiella (Rebel, 1915)
    subtilipennis (Turati, 1924)
Mesophleps ochracella (Turati, 1926)
    orientella Nel & Nel, 2003
    gallicella Varenne & Nel, 2011

Chelariini Le Marchand, 1947
    Hypatimini Kloet & Hincks, 1945, unavailable
    Anarsiini Amsel, 1977

***Nothris* Hübner, 1825 [19]**
Nothris congressariella (Bruand, 1858)
    declaratella Staudinger, 1859
Nothris lemniscellus (Zeller, 1839)
Nothris gregerseni Karsholt & Šumpich, 2015 **[20]**
Nothris verbascella ([Denis & Schiffermüller], 1775)
    discretella Rebel, 1889
    clarella Amsel, 1935
Nothris sulcella Staudinger, 1879
    magna Nel & Peslier, 2007
Nothris radiata (Staudinger, 1879) **[21]**
Nothris skyvai Karsholt & Šumpich, 2015

***Neofaculta* Gozmány, 1955**
    Haplovalva Janse, 1958
Neofaculta ericetella (Geyer, 1832) **[22]**
    gallinella (Treitschke, 1833)
    lanceolella (Stephens, 1834)
    fuscella (Duponchel, 1844)
    subatrella (Duponchel, 1845)
    quinquemaculella (Bruand d'Uzelle, 1859)
    orcella (Zerny, 1927), subspecies
    atlanticella (Amsel, 1938), subspecies
    tenalella (Amsel, 1938)
    amseli (Dufrane, 1955)
    pyrenemontana (Dufrane, 1955)
    betulea auct.
Neofaculta infernella (Herrich-Schäffer, 1854)
    infernalis, unavailable
Neofaculta taigana Ponomarenko, 1998 **[23]**

***Hypatima* Hübner, 1825**
    Chelaria Haworth, 1828
    Tituacia Walker, 1864
    Stomylia Snellen, 1878
    Allocota Meyrick, 1904, homonym
    Cymatomorpha Meyrick, 1904
    Deuteroptila Meyrick, 1904
    Semodictis Meyrick, 1909
    Allocotaniana Strand, 1913
    Episacta Turner, 1919
Hypatima rhomboidella (Linnaeus, 1758) **[24]**
    conscriptella (Hübner, 1805)

hubnerella (Donovan, 1806), incorrect original spelling
huebnerella (Donovan, 1806), justified emendation
conscripta Haworth, 1828, emendation

Anarsia Zeller, 1839 [25]
 Ananarsia Amsel, 1959
Anarsia lineatella Zeller, 1839
 pullatella (Hübner, 1796), nomen oblitum
 pruniella Clemens, 1860
 heratella Amsel, 1967, subspecies
 tauricella Amsel, 1967, subspecies
Anarsia innoxiella Gregersen & Karsholt, 2017
Anarsia spartiella (Schrank, 1802)
 robertsonella (Curtis, 1837)
 genistae Stainton, 1854
 genistella Doubleday, 1859, emendation
 ragonotella Réal, 1994
 krausei Réal, 1994
 lhommella Réal, 1994
 acutiloba Réal, 1994
 pseudospartiella Réal, 1994
 ungemachi Réal, 1994
Anarsia bilbainella (Rössler, 1877) **[26]**
 burmanni Amsel, 1958
 bizensis Réal, 1994
 infundiblulella Réal, 1994
 ovilella Réal, 1994
Anarsia eleagnella Kuznetsov, 1957
Anarsia dejoannisi Réal, 1994
Anarsia leberonella Réal, 1994
Anarsia sibirica Park & Ponomarenko, 1996
Anarsia stepposella Ponomarenko, 2002
psammobia Falkovitsh & Bidzilya, 2003
Anarsia acaciae Walsingham, 1896
Anarsia balioneura Meyrick, 1921

Dichomeridinae Hampson, 1918
 Brachminae Omelko, 1999
 Dichomerinae, misspelling

Dichomeris Hübner, 1818 [27]
 Elasmion Hübner, 1808, unavailable
 Oxybelia Hübner, 1825

  Rhinosia Treitschke, 1833
  Gaesa Walker, 1864
  Uliaria Dumont, 1921
  Cymotricha Meyrick, 1923
  Acanthophila Heinemann, 1870
  Mimomeris Povolný, 1978
Dichomeris acuminatus (Staudinger, 1876)
  ianthes (Meyrick, 1887)
  rusticus (Walsingham, 1892)
  lotellus (Constant, 1893)
  ammoxanthus (Meyrick, 1904)
  ochrophanes (Meyrick, 1907)
  sublotellus (Caradja, 1920)
Dichomeris cisti (Staudinger, 1859)
  meridionella (Walsingham, 1891)
Dichomeris limbipunctellus (Staudinger, 1859) **[28]**
  millierellus Stainton, 1873
Dichomeris neatodes Meyrick, 1923 **sp. rev. [28]**
Dichomeris helianthemi (Walsingham, 1903)
Dichomeris castellana (Schmidt, 1941)
Dichomeris juniperella (Linnaeus, 1761) **[29]**
  juniperi Haworth, 1828, emendation
Dichomeris marginella (Fabricius, 1781)
  fimbriella (Thunberg, 1788)
  clarella (Treitschke, 1833)
Dichomeris ustalella (Fabricius, 1794)
  capucinella (Hübner, 1796)
  cornutus (Fabricius, 1798)
  ustulatus (Fabricius, 1798), emendation
  burgundiellus (Bruand d'Uzelle, 1859)
Dichomeris derasella ([Denis & Schiffermüller], 1775)
  fasciella (Hübner, 1796)
  unguiculatus (Fabricius, 1798)
  coreanus Matsumura, 1931
  paranthes Meyrick, 1936
Dichomeris limosellus (Schläger, 1849)
  deflectivellus (Reutti, 1853)
Dichomeris nitiellus (Costantini, 1923)
Dichomeris rasilella (Herrich-Schäffer, 1854) **[30]**
  lacrimella (Caradja, 1920)
  insulella (Dumont, 1921)
  occidentella (Zerny, 1927), subspecies
Dichomeris barbella ([Denis & Schiffermüller], 1775)

Dichomeris alacella (Zeller, 1839)
Dichomeris latipennella (Rebel, 1937)
　　scotosiella (Hackman, 1945)
　　piceana (Šulcs, 1968)
　　steueri Povolný, 1978

Anasphaltis Meyrick, 1925
Anasphaltis renigerellus (Zeller, 1839)

Acompsia Hübner, 1825 [31]
　　Brachycrossata Heinemann, 1870
　　Telephila Meyrick, 1923
Acompsia cinerella (Clerck, 1759)
　　murinella (Scopoli, 1763)
　　ardeliella (Hübner, 1817)
　　cinerea (Haworth, 1828), emendation
　　spodiella (Treitschke, 1833)
Acompsia pyrenaella Huemer & Karsholt, 2002 **[32]**
Acompsia antirrhinella Millière, 1866 **[33]**
Acompsia baldizzonei Pinzari, Nel & Pinzari, 2016
Acompsia maculosella (Stainton, 1851) **[34]**
Acompsia dimorpha Petry, 1904
Acompsia subpunctella Svensson, 1966
Acompsia delmastroella Huemer, 1998
Acompsia muellerrutzi Wehrli, 1925
Acompsia caucasella Huemer & Karsholt, 2002
Acompsia minorella Rebel, 1899
Acompsia tripunctella ([Denis & Schiffermüller], 1775) **[35]**
Acompsia ponomarenkoae Huemer & Karsholt, 2002
Acompsia schmidtiellus (Heyden, 1848)
　　durdhamellus (Stainton, 1849)
　　quadrinella (Herrich-Schäffer, 1854)

Brachmia Hübner, 1825 [36]
　　Claododes Heinemann, 1870, homonym
　　Eudodacles Snellen, 1889
　　Aulacomima Meyrick, 1904
　　Apethistis Meyrick, 1908
Brachmia dimidiella ([Denis & Schiffermüller], 1775) **[37]**
　　costiguttella (Lienig & Zeller, 1846)
　　kneri (Nowicki, 1864)
Brachmia blandella (Fabricius, 1798)
　　gerronella (Zeller, 1850)

Brachmia procursella Rebel, 1903
Brachmia inornatella (Douglas, 1850)

Helcystogramma Zeller, 1877
  Ceratophora Heinemann, 1870, homonym
  Dectobathra Meyrick, 1904
  Teuchophanes Meyrick, 1914
  Schemataspis Meyrick, 1918
  Parelectra Meyrick, 1925, homonym
  Psamathoscopa Meyrick, 1937
  Anathyrsotis Meyrick, 1939
  Parelectroides Clarke, 1952
  Onebala auct.
Helcystogramma lineolella (Zeller, 1839)
Helcystogramma triannulella (Herrich-Schäffer, 1854)
  sepiella (Steudel, 1866)
  cinerea (Caradja, 1931)
  macroscopa (Meyrick, 1932)
Helcystogramma lutatella (Herrich-Schäffer, 1854)
Helcystogramma rufescens (Haworth, 1828)
  simplella (Eversmann, 1844)
  diaphanella (Lienig & Zeller, 1846)
  isabella (Stainton, 1849)
  rufescentella (Doubleday, 1859), emendation
Helcystogramma albinervis (Gerasimov, 1929)
Helcystogramma arulensis (Rebel, 1929)
Helcystogramma klimeschi Ponomarenko & Huemer, 2001
Helcystogramma flavescens Junnilainen, 2010
Helcystogramma convolvuli (Walsingham, 1908)
  chrypsilychna (Meyrick, 1914)
  dryadopa (Meyrick, 1918)
  effera (Meyrick, 1918)
  emigrans (Meyrick, 1921)
Helcystogramma lamprostoma (Zeller, 1847) **[38]**
  scutata (Meyrick, 1894)

Pseudosophronia Corley, 2001 [39]
Pseudosophronia exustellus (Zeller, 1847)
  catharurga Meyrick, 1923
  parahumerella Amsel, 1935
  buvati Nel, 1998
  constanti Nel, 1998, **syn. nov.**
Pseudosophronia cosmella (Constant, 1885)

Apatetrinae Le Marchand, 1947
Chrysoesthiinae Paclt, 1947, unavailable

Pexicopiini Hodges, 1986

Harpagidia **Ragonot, 1895**
Glaphyrerga Meyrick, 1925
Harpagidia magnetella (Staudinger, 1871)
pallidibasella Ragonot, 1895
melitophanes (Meyrick, 1931)

Pectinophora **Busck, 1917**
Pectinophora gossypiella (Saunders, 1844)

Pexicopia **Common, 1958**
Pexicopia malvella (Hübner, 1805) **[40]**
lutarea (Haworth, 1828), unavailable
umbrella auct.

Platyedra **Meyrick, 1895**
Aratrognathosia Gozmány, 1968, unavailable
Platyedra subcinerea (Haworth, 1828)
vilella (Zeller, 1847)
parviocellatella (Bruand d'Uzelle, 1851)
bathrosticta (Meyrick, 1937)

Sitotroga **Heinemann, 1870**
Nesolechia Meyrick, 1921
Syngenomictis Meyrick, 1927
Sitotroga psacasta Meyrick, 1908
celyphodes (Meyrick, 1909)
nea Walsingham, 1920
Sitotroga cerealella (Olivier, 1789)
hordei (Kirby, 1815)
arctella (Walker, 1864)
melanarthra (Lower, 1900)
palearis (Meyrick, 1913)
aenictopa (Meyrick, 1927)
ochrescens (Meyrick, 1938)
asemodes (Meyrick, 1938)

Apatetrini Le Marchand, 1947 [41]

***Dactylotula* Cockerell, 1888**
  Dactylota Snellen, 1876, homonym
  Didactylota Walsingham, 1892
  Rotundivalva Janse, 1951
Dactylotula altithermella (Walsingham, 1903)
Dactylotula kinkerella (Snellen, 1876) **[42]**

***Apatetris* Staudinger, 1879 [43]**
Apatetris agenjoi Gozmány, 1954
Apatetris mediterranella Nel & Varenne, 2012 **[44]**

***Catatinagma* Rebel, 1903**
Catatinagma trivittellum Rebel, 1903 **[45]**
Catatinagma kraterella Junnilainen & Nupponen, 2010 **[46]**

***Coloptilia* Fletcher, 1940**
  Colopteryx Hofmann, 1898, homonym
Coloptilia conchylidella (Hofmann, 1898)

***Chrysoesthia* Hübner, 1825 [47]**
  Microsetia Stephens, 1829
  Chrysia Bruand d'Uzelle, 1851
  Nomia Clemens, 1860, homonym
  Chrysopora Clemens, 1860
  Nannodia Heinemann, 1870
  Anaphaula Walsingham, 1904
Chrysoesthia drurella (Fabricius, 1775) **[48]**
  myllerella (Fabricius, 1794)
  zinckenlla (Hübner, 1813)
  druryella (Zeller, 1851), emendation
  hermannella auct.
Chrysoesthia eppelsheimi (Staudinger, 1885)
Chrysoesthia verrucosa Tokár, 1999
Chrysoesthia sexguttella (Thunberg, 1794)
  auropunctella (Thunberg, 1794)
  aurofasciella (Stephens, 1834)
  naeviferella (Duponchel, 1843)
  stipella auct.
Chrysoesthia halimionella Bidzilya & Budashkin, 2015
Chrysoesthia atriplicella (Amsel, 1939) **[49]**
Chrysoesthia gaditella (Staudinger, 1859) **[49]**
Chrysoesthia aletris (Walsingham, 1919) **[49]**

Chrysoesthia boseae (Walsingham, 1908)
Chrysoesthia falkovitshi Lvovsky & Piskunov, 1989
Chrysoesthia hispanica Karsholt & Vives, 2014

Metanarsia Staudinger, 1871
    Calyptrotis Meyrick, 1891
    Epipararsia Rebel, 1914
    Parametanarsia Gerasimov, 1930
Metanarsia modesta Staudinger, 1871 **[50]**
    kurdistanella Amsel, 1959, subspecies
Metanarsia onzella Christoph, 1887
Metanarsia guberlica Nupponen, 2010
Metanarsia incertella (Herrich-Schäffer, 1861)
    longivitella (Rebel, 1914)
    halmyropis (Meyrick, 1926)
    ramiferella (Lucas, 1940)

Oecocecis Guenée, 1870
Oecocecis guyonella Guenée, 1870 **[51]**

Thiotrichinae Karsholt, Mutanen, Lee & Kaila, 2013 [52]
    Palumbininae Chapman, 1902, *nomen nudum*

Thiotricha Meyrick, 1886
    Reuttia Hofmann, 1898
    Mystax Caradja, 1920, homonym
Thiotricha majorella Rebel, 1910
Thiotricha subocellea (Stephens, 1834)
    internella (Lienig & Zeller, 1846)
    dissonella (Herrich-Schäffer, 1854)
    subocellella (Doubleday, 1859), emendation
Thiotricha coleella (Constant, 1885)
Thiotricha wollastoni (Walsingham, 1884)

Palumbina Rondani, 1876
    Thyrsostoma Meyrick, 1907
Palumbina guerinii (Stainton, 1858)
    terebintella Rondani, 1876
    pistaciae (Anagnostopoulos, 1935)

Anomologinae Meyrick, 1926
    Aristoteliinae Le Marchand, 1947
    Metzneriini Piskunov, 1975

Isophrictini Povolný, 1979

***Bryotropha* Heinemann, 1870 [53]**
   Mniophaga Pierce & Daltry, 1938
   Adelphotropha Gozmány, 1955
Bryotropha sabulosella (Rebel, 1905)
Bryotropha domestica (Haworth, 1828)
   domesticella (Doubleday, 1859), emendation
   punctata (Staudinger, 1876)
   salmonis (Walsingham, 1908)
   algiricella Chrétien, 1917
Bryotropha vondermuhlli Nel & Brusseaux, 2003
Bryotropha rossica Anikin & Piskunov, 1996
   tachengensis Li & Zheng, 1997
Bryotropha azovica Bidzilia, 1997
Bryotropha arabica Amsel, 1952
Bryotropha patockai Elsner & Karsholt, 2003
Bryotropha purpurella (Zetterstedt, 1839)
   flavipalpella (Nylander, 1848)
Bryotropha tachyptilella (Rebel, 1916)
Bryotropha italica Karsholt & Rutten, 2005
Bryotropha politella (Stainton, 1851)
   expolitella (Doubleday, 1859)
Bryotropha aliterrella (Rebel, 1935)
Bryotropha nupponeni Karsholt & Rutten, 2005
Bryotropha satschkovi Anikin & Piskunov, 2018
Bryotropha terrella ([Denis & Schiffermüller], 1775) **[54]**
   inulella (Hübner, 1805)
   pauperella (Hübner, 1825)
   latella (Herrich-Schäffer, 1854)
   lutescens (Constant, 1865)
   suspectella (Heinemann, 1870)
   alpicolella Heinemann, 1870
   tenebrosella (Teich, 1886)
   sardoterrella Schawerda, 1936
   quignoni Dufrane, 1938, unavailable
   joannisi Dufrane, 1938, unavailable
   rufa Dufrane, 1938, unavailable
   ochrea Dufrane, 1938, unavailable
Bryotropha sattleri Nel, 2003
Bryotropha desertella (Douglas, 1850) **[55]**
   decrepidella (Herrich-Schäffer, 1854)
   glabrella Heinemann, 1870

Bryotropha wolschrijni Karsholt & Rutten, 2005
Bryotropha heckfordi Karsholt & Rutten, 2005
Bryotropha figulella (Staudinger, 1859)
　capnella (Constant, 1865)
　cinnamomea Turati, 1934
Bryotropha plantariella (Tengström, 1848)
　cinerosella (Tengström, 1848)
　serrulatella (Tengström, 1848)
　brevipalpella Rebel, 1893
Bryotropha galbanella (Zeller, 1839)
　angustella (Heinemann, 1870)
　ilmatariella (Hoffmann, 1893)
　griseella (Caradja, 1920)
　haareki (Strand, 1920)
　fusconigratella (Palm, 1947)
Bryotropha boreella (Douglas, 1851)
Bryotropha sutteri Karsholt & Rutten, 2005
Bryotropha gallurella Amsel, 1952
Bryotropha hendrikseni Karsholt & Rutten, 2005
Bryotropha pallorella Amsel, 1952
　mulinoides Amsel, 1952
　zannonicola Hartig, 1953
Bryotropha hulli Karsholt & Rutten, 2005 **[56]**
Bryotropha plebejella (Zeller, 1847)
　imperitella (Staudinger, 1859)
　ancillula (Walsingham, 1908)
　inexpectella Nel, 1999
Bryotropha dryadella (Zeller, 1850)
　saralella Amsel, 1952
Bryotropha basaltinella (Zeller, 1839)
Bryotropha affinis (Haworth, 1828) **[57]**
　tegulella (Herrich-Schäffer, 1854)
　tectella (Herrich-Schäffer, 1854)
　affinella (Doubleday, 1859), emendation
　affinitella (Bruand d'Uzelle, 1859), emendation
Bryotropha umbrosella (Zeller, 1839) **[58]**
　mundella (Douglas, 1850)
　portlandicella (Richardson, 1890)
　fulvipalpella Joannis, 1908
　anacampsoidella (Hering, 1924)
　oppositella auct.
Bryotropha similis (Stainton, 1854)

  thuleella (Zeller, 1857)
  similella (Doubleday, 1859), emendation
  pullifimbriella (Clemens, 1863)
  confinis (Stainton, 1871)
  obscurecinerea (Nolcken, 1871)
  stolidella (Morris, 1872)
  fuliginosella (Snellen, 1882)
  tahavusella (Forbes, 1922)
  clandestina (Meyrick, 1923)
  dufraneella (Joannis, 1928)
  novisimilis Li & Zheng, 1997
Bryotropha senectella (Zeller, 1839)
  ciliatella (Herrich-Schäffer, 1854)
  obscurella Heinemann, 1870
  minorella Heinemann, 1870
  phoebusella Millière, 1876
  larseni Strand, 1927

Epidola **Staudinger, 1859 [59]**
Epidola stigma Staudinger, 1859
Epidola barcinonella Millière, 1867
Epidola semitica Amsel, 1942 **[60]**
Epidola nuraghella Hartig, 1939
Epidola melitensis Amsel, 1955

Aristotelia **Hübner, 1825 [61]**
  Ergatis Heinemann, 1870, homonym
  Eucatoptus Walsingham, 1897
Aristotelia decurtella (Hübner, 1813) **[62]**
  turbatella (Treitschke, 1835)
  amoenella (Joannis,1891)
Aristotelia decoratella (Staudinger, 1879)
Aristotelia leonhardi Krone, 1907
Aristotelia ericinella (Zeller, 1839) **[63]**
  silendrella Caradja, 1920, unavailable
Aristotelia subdecurtella (Stainton, 1859) **[64]**
Aristotelia subericinella (Duponchel, 1843) **[65]**
  prohaskaella (Rebel, 1907)
Aristotelia billii Varenne & Nel, 2013 **[66]**
Aristotelia montarcella Schmidt, 1941
Aristotelia heliacella (Herrich-Schäffer, 1854)
  rogenhoferi (Staudinger, 1872)

Aristotelia pancaliella (Staudinger, 1871)
Aristotelia baltica Šulcs & Šulcs, 1983
    coeruleopictella auct.
Aristotelia brizella (Treitschke, 1833)
Aristotelia brizelloidea Amsel, 1935
Aristotelia confusella Bidzilya & Budashkin, 2015
Aristotelia staticella Millière, 1876
Aristotelia mirandella Chrétien, 1908
Aristotelia frankeniae Walsingham, 1898
Aristotelia calastomella (Christoph, 1873)
Aristotelia mirabilis (Christoph, 1888)

Caulastrocecis Chrétien, 1931 [67]
    Caulastrocecis pudicellus (Mann, 1861)
    apicella (Caradja, 1920)
Caulastrocecis gypsella (Constant, 1893)
Caulastrocecis furfurella (Staudinger, 1871) **[68]**
Caulastrocecis cryptoxena (Gozmány, 1952) **sp. rev. [68]**
Caulastrocecis perexigella Junnilainen, 2010
Caulastrocecis interstratella (Christoph, 1873)
    salinatrix (Meyrick, 1926)

Paranarsia Ragonot, 1895 [69]
Paranarsia joannisiella Ragonot, 1895

Megacraspedus Zeller, 1839 [70]
    Chilopselaphus Mann, 1867
    Chilopsephalus Rebel, 1901, misspelling
    Toxoceras Chrétien, 1915, homonym
    Toxidoceras Chrétien, 1923
    Nevadia Caradja, 1920, homonym
    Cauloecista Dumont, 1928
    Reichardtiella Filipjev, 1931
    Vadenia Caradja, 1933
Megacraspedus lanceolellus (Zeller, 1850) **[71]**
    subdolellus Staudinger, 1859
    hessleriellus Rössler, 1868
    tutti Walsingham, 1897
    grossisquammellus Chrétien, 1925
Megacraspedus bengtssoni Huemer & Karsholt, 2018
Megacraspedus junnilaineni Huemer & Karsholt, 2018
Megacraspedus uzunsyrtus Bidzilya & Budashkin, 2015
Megacraspedus similellus Huemer & Karsholt, 2018

Megacraspedus tokari Huemer & Karsholt, 2018
Megacraspedus dolosellus (Zeller, 1839) **[72]**
   separatellus (Fischer von Röslerstamm, 1843)
   incertellus Rebel, 1930
Megacraspedus neli Huemer & Karsholt, 2018
Megacraspedus faunierensis Huemer & Karsholt, 2018
Megacraspedus gredosensis Huemer & Karsholt, 2018
Megacraspedus cuencellus Caradja, 1920
Megacraspedus bidentatus Huemer & Karsholt, 2018
Megacraspedus fuscus Huemer & Karsholt, 2018
Megacraspedus trineae Huemer & Karsholt, 2018
Megacraspedus tristictus Walsingham, 1910
Megacraspedus alfacarellus Wehrli, 1926
Megacraspedus pusillus Walsingham, 1903
Megacraspedus skoui Huemer & Karsholt, 2018
Megacraspedus spinophallus Huemer & Karsholt, 2018 **[73]**
Megacraspedus occidentellus Huemer & Karsholt, 2018
Megacraspedus granadensis Huemer & Karsholt, 2018
Megacraspedus heckfordi Huemer & Karsholt, 2018
Megacraspedus tenuiuncus Huemer & Karsholt, 2018
Megacraspedus lativalvellus Amsel, 1954
Megacraspedus dejectella (Staudinger, 1859)
Megacraspedus devorator Huemer & Karsholt, 2018
Megacraspedus binotella (Duponchel, 1843) **[74]**
Megacraspedus brachypteris Huemer & Karsholt, 2018 **[75]**
Megacraspedus barcodiellus Huemer & Karsholt, 2018
Megacraspedus bilineatella Huemer & Karsholt, 1996
Megacraspedus andreneli Varenne & Nel, 2014 **[76]**
Megacraspedus sumpichi Huemer & Karsholt, 2018
Megacraspedus gallicus Huemer & Karsholt, 2018
Megacraspedus ribbeella (Caradja, 1920)
Megacraspedus numidellus (Chrétien, 1915)
   mareotidellus Turati, 1924,
Megacraspedus albovenata Junnilainen, 2010
Megacraspedus longipalpella Junnilainen, 2010
Megacraspedus niphorrhoa (Meyrick, 1926)
Megacraspedus fallax (Mann, 1867)
Megacraspedus balneariellus (Chrétien, 1907)
Megacraspedus podolicus (Toll, 1942)
Megacraspedus knudlarseni Huemer & Karsholt, 2018
Megacraspedus imparellus (Fischer v. Röslerstamm, 1843) **[77]**
   litovalvellus Junnilainen, 2010
Megacraspedus multispinella Junnilainen & Nupponen, 2010

Megacraspedus cerussatellus Rebel, 1930
Megacraspedus attritellus Staudinger, 1871
Megacraspedus lagopellus (Herrich-Schäffer, 1860)
Megacraspedus argyroneurellus Staudinger, 1871
Megacraspedus ibericus Huemer & Karsholt, 2018
Megacraspedus squalida Meyrick, 1926
   escalerellus Schmidt, 1941
Megacraspedus pentheres Walsingham, 1920
Megacraspedus teriolensis Huemer & Karsholt, 2018 **[78]**
Megacraspedus korabicus Huemer & Karsholt, 2018
Megacraspedus quadristictus Lhomme, 1946
Megacraspedus eburnellus Huemer & Karsholt, 2001
Megacraspedus skulei Huemer & Karsholt, 2018
Megacraspedus peyerimhoffi Le Cerf, 1925
Megacraspedus peslieri Huemer & Karsholt, 2018

Dirhinosia Rebel, 1905 [79]
Dirhinosia cervinella (Eversmann, 1844)
   trifasciella Rebel, 1905
Dirhinosia arnoldiella (Rebel, 1905)
Dirhinosia interposita Bidzilya & Budashkin, 2015

Psamathocrita Meyrick, 1925 [80]
Psamathocrita osseella (Stainton, 1860)
Psamathocrita argentella Pierce & Metcalfe, 1942
Psamathocrita dalmatinella Huemer & Tokár, 2000

Chimericorsa Varenne, Huemer & Nel, 2017
Chimericorsa nioloensis Varenne, Huemer & Nel, 2017

Spiniphallellus Bidzilya & Karsholt, 2008
Spiniphallellus desertus Bidzilya & Karsholt, 2008
Spiniphallellus chrysotosella Junnilainen, 2016

Deltophora Janse, 1950
Deltophora maculata (Staudinger, 1879)
Deltophora stictella (Rebel, 1927)
Deltophora gielisia Hull, 1995

Ivanauskiella Ivinskis & Piskunov, 1980 [81]
Spatuncusella Nel & Varenne, 2013
Ivanauskiella psamathias (Meyrick, 1891)
   turkmenica auct.
Ivanauskiella occitanica (Nel & Varenne, 2013) **sp. rev. [82]**

***Ptocheuusa* Heinemann, 1870 [83]**
   Syneunetis Wallengren, 1881
Ptocheuusa paupella (Zeller, 1847) **[84]**
   inulella (Curtis, 1850)
   melanolepidella (Heydenreich, 1851)
   perniveella (Bruand d'Uzelle, 1859)
Ptocheuusa inopella (Zeller, 1839) **[85]**
   amesella Chrétien, 1908
Ptocheuusa abnormella (Herrich-Schäffer, 1854)
Ptocheuusa minimella (Rebel, 1936)
Ptocheuusa asterisci (Walsingham, 1903)
Ptocheuusa scholastica (Walsingham, 1903)
Ptocheuusa guimarensis (Walsingham, 1908)
Ptocheuusa sublutella Christoph, 1873
Ptocheuusa cinerella (Chrétien, 1908) **comb. nov. [86]**

***Gladiovalva* Sattler, 1960**
Gladiovalva rumicivorella (Millière, 1881)
Gladiovalva aizpuruai Vives, 1990
Gladiovalva badidorsella (Rebel, 1935)

***Ornativalva* Gozmány, 1955**
   Pelostola Janse, 1960
Ornativalva heluanensis (Debski, 1913)
   frankeniivorella (Chrétien, 1917)
   oasicolella (Turati, 1924)
   siculella (Mariani, 1937)
Ornativalva ornatella Sattler, 1967
Ornativalva tamariciella (Zeller, 1850)
Ornativalva pseudotamariciella Sattler, 1967
Ornativalva antipyramis (Meyrick, 1925)
Ornativalva plutelliformis (Staudinger, 1859)
   olbiaella (Millière, 1861)
   siewersiellus (Christoph, 1867)
   sinuatella (Walsingham, 1904)
Ornativalva sieversi (Staudinger, 1871)
Ornativalva mixolitha (Meyrick, 1918)
   bipunctella (Sattler, 1967), subspecies

***Atremaea* Staudinger, 1871**
   Calamotypa Meyrick, 1926
Atremaea lonchoptera Staudinger, 1871
   exstans (Meyrick, 1926)

***Amblypalpis* Ragonot, 1886 [87]**
Amblypalpis olivierella Ragonot, 1887

***Parapodia* Joannis, 1912 [88]**
   Cecidonostola Amsel, 1958
Parapodia sinaica (Frauenfeld, 1860)
   tamaricicola Joannis, 1912
   tamariciella (Amsel, 1958)

***Isophrictis* Meyrick, 1917 [89]**
Isophrictis robinella (Chrétien, 1907)
   microlina Meyrick, 1935
Isophrictis meridionella (Herrich-Schäffer, 1854)
Isophrictis constantina (Baker, 1888)
Isophrictis cerdanica Nel, 1995
Isophrictis lineatellus (Zeller, 1850)
   albilineella (Bruand d´Uzelle, 1859)
Isophrictis kefersteiniellus (Zeller, 1850) **[90]**
   senicula (Meyrick, 1913)
Isophrictis striatella ([Denis & Schiffermüller], 1775)
   tanacetella (Schrank, 1802)
   substriatella (Caradja, 1920), subspecies
Isophrictis corsicella Amsel, 1936
Isophrictis invisella (Constant, 1885)
Isophrictis anthemidella (Wocke, 1871) **[91]**
Isophrictis impugnata Gozmány, 1957

***Pyncostola* Meyrick, 1917**
Pyncostola bohemiella (Nickerl, 1864)
   tunesiella (Chrétien, 1915)
   jablonkayi (Gozmány, 1954)

***Metzneria* Zeller, 1839 [92]**
   Cleodora Stephens, 1834, homonym
   Parasia Duponchel, 1846
   Archimetzneria Amsel, 1936
Metzneria paucipunctella (Zeller, 1839)
   zimmermanni Hering, 1940
   confusalis Lucas, 1956
   luqueti Nel, 1995
Metzneria tenuiella (Mann, 1864)
   seminivora (Walsingham, 1903)
   infelix Walsingham, 1908

insignificans Walsingham, 1908
Metzneria neuropterella (Zeller, 1839)
   nevropterella (Duponchel, 1843) **[93]**
   gigantella Krulikowsky, 1909, unavailable
Metzneria aestivella (Zeller, 1839) **[94]**
   carlinella (Stainton, 1851)
   selaginella (Mann, 1855)
   torridella (Mann, 1859)
   dichroa Walsingham, 1908, subspecies.
   expositoi Vives, 2001, **syn. nov.**
Metzneria lappella (Linnaeus, 1758)
Metzneria castiliella (Möschler, 1866)
   eatoni Walsingham, 1899
Metzneria littorella (Douglas, 1850)
   quinquepunctella (Herrich-Schäffer, 1854)
Metzneria riadella Englert, 1974
Metzneria diffusella Englert, 1974
Metzneria fulva Labonne, Huemer, Thibault & Nel, 2019 **[95]**
Metzneria torosulella (Rebel, 1893) **[95]**
   monochroa Walsingham, 1908
   ignota Turati, 1922
Metzneria ehikeella Gozmány, 1954 **[96]**
Metzneria metzneriella (Stainton, 1851) **[97]**
   falcatella (Bruand d´Uzelle, 1859)
Metzneria hilarella Caradja, 1920
Metzneria staehelinella Englert, 1974
Metzneria artificella (Herrich-Schäffer, 1861) **[98]**
   litigiosella (Millière, 1879)
   pannonicella Rebel, 1915
Metzneria agraphella (Ragonot, 1895)
   incognita Walsingham, 1904
Metzneria aprilella (Herrich-Schäffer, 1854) **[99]**
   igneella (Tengström, 1859)
   sanguinolentella Joannis, 1910
Metzneria subflavella Englert, 1974 **[100]**
Metzneria filia Piskunov, 1979
Metzneria intestinella (Mann, 1864)
Metzneria santolinella (Amsel, 1936)
   consimilella Hackman, 1946
Metzneria tristella Rebel, 1901
Metzneria campicolella (Mann, 1857) **[101]**
   varennei Nel, 1997

***Apodia* Heinemann, 1870**
Apodia bifractella (Duponchel, 1843)
　　inulella (Vallot, 1829), homonym
Apodia martinii Petry, 1911 **sp. rev. [102]**

***Pragmatodes* Walsingham, 1908 [103]**
Pragmatodes fruticosella Walsingham, 1908
Pragmatodes melagonella (Constant, 1895) **comb. nov. [103, 104]**
Pragmatodes albagonella (Varenne & Nel, 2010) **comb. nov. [103]**
Pragmatodes cyrneogonella (Nel & Varenne, 2012) **comb. nov. [103]**
Pragmatodes parvulata (Gozmány, 1953) **comb. nov. [103]**
　　mediterranea (Nel & Luquet, 1997)

***Argolamprotes* Benander, 1945**
Argolamprotes micella ([Denis & Schiffermüller], 1775)
　　asterella (Treitschke, 1833)

***Monochroa* Heinemann, 1870 [105]**
　　Paltodora Meyrick, 1894
　　Catabrachmia Rebel, 1909
Monochroa rumicetella (Hofmann, 1868) **[106]**
　　acutangulella (Heinemann, 1870)
　　leptotechna (Meyrick, 1937)
Monochroa rebeli (Hering, 1927)
Monochroa sepicolella (Herrich-Schäffer, 1854) **[107]**
Monochroa rectifasciella (Fuchs, 1902) **[107]**
Monochroa tenebrella (Hübner, 1817) **[108]**
　　fuscocuprea (Haworth, 1828)
　　subcuprella (Stephens, 1834)
　　tenebrosella (Zeller, 1839)
　　parvella (Heydenreich, 1851)
　　fuscocuprella Doubleday, 1859, emendation
　　buffonella (Millière, 1876)
Monochroa scutatella (Müller-Rutz, 1920)
Monochroa dellabeffai (Rebel, 1932)
Monochroa servella (Zeller, 1839) **[109]**
　　farinosae (Stainton,1867)
Monochroa conspersella (Herrich-Schäffer, 1854)
　　questionella (Herrich-Schäffer, 1854)
　　morosa (Mühlig, 1864)
Monochroa tetragonella (Stainton, 1885)
　　gudmanni (Larsen, 1927)
Monochroa elongella (Heinemann, 1870)

micrometra (Meyrick, 1935)
Monochroa inflexella Svensson, 1992
Monochroa sperata Huemer & Karsholt, 2010
Monochroa lutulentella (Zeller, 1839)
   brunickii (Rebel, 1913)
Monochroa aenigma Anikin & Piskunov, 2018
Monochroa saltenella (Benander, 1928)
Monochroa palustrellus (Douglas, 1850)
   rozsikella (Rebel, 1909)
Monochroa divisella (Douglas, 1850)
   csornensis Rebel, 1909
   lepidolampra (Gozmány, 1952)
   zarichella Piskunov, 1975
Monochroa lucidella (Stephens, 1834) **[110]**
   scordiscella (Rebel, 1904)
   unipunctella (Amsel, 1935)
   immaculatella Huemer, 1996, subspecies
Monochroa simplicella (Lienig & Zeller, 1846)
   impella (Piskunov, 1975)
Monochroa moyses Uffen, 1991
Monochroa arundinetella (Boyd, 1857) **[111]**
Monochroa suffusella (Douglas, 1850) **[111]**
   oblitella (Doubleday, 1859)
   peterseni (Teich, 1901)
Monochroa cytisella (Curtis, 1837)
   fuscipennis (Humphreys & Westwood, 1845)
   walkeriella (Douglas, 1850)
   coenulentella (Herrich-Schäffer, 1854)
   clinosema (Meyrick, 1935)
   griseocapitella (Bentinck, 1949), unavailable
Monochroa ferrea (Frey, 1870)
   latiuscula (Heinemann, 1870)
   alfkeni (Amsel, 1938)
   servella auct.
Monochroa nomadella (Zeller, 1868) **[112]**
Monochroa bronzella Karsholt, Nel, Fournier, Varenne & Huemer, 2013
Monochroa hornigi (Staudinger, 1883)
   leptocrossa (Meyrick, 1926)
   nordmanella Bruun, 1958
Monochroa niphognatha (Gozmány, 1953)

***Oxypteryx* Rebel, 1911 [113]**
   Eulamprotes Bradley, 1971

Lamprotes Heinemann, 1870, homonym
Argyritis Heinemann, 1870, homonym
Siderea Omelko, 1999
Oxypteryx nigromaculella (Millière, 1872) **comb. nov. [113, 114]**
  punctatella (Staudinger, 1879)
  morphochroma (Walsingham, 1900)
  jactatrix (Meyrick, 1926)
  angustipennis (Rebel, 1931)
  craterotypa (Meyrick, 1939)
  donskoffi (Nel & Luquet, 1997)
Oxypteryx wilkella (Linnaeus, 1758) **comb. nov. [113, 115]**
  merianella (Linnaeus, 1758)
  germarella (Geyer, 1832)
  pictella (Zeller, 1839)
  tarquiniella (Stainton, 1862)
Oxypteryx ochricapilla (Rebel, 1903) **comb. nov. [113]**
Oxypteryx superbella (Zeller, 1839) **comb. nov. [113]**
Oxypteryx mirusella (Huemer & Karsholt, 2013) **comb. nov. [113]**
Oxypteryx baldizzonei (Karsholt & Huemer, 2013) **comb. nov. [113, 116]**
Oxypteryx occidentella (Huemer & Karsholt, 2011) **comb. nov. [113]**
Oxypteryx libertinella (Zeller, 1872) **comb. nov. [113, 117]**
Oxypteryx gemerensis (Elsner, 2013) **comb. nov. [113]**
Oxypteryx deserta (Piskunov, 1990) **comb. nov. [113]**
Oxypteryx unicolorella (Duponchel, 1843) **comb. nov. [113]**
  lucentella (Peyerimhoff, 1870)
Oxypteryx atrella ([Denis & Schiffermüller], 1775)
  quadripunctella (Fabricius, 1781)
  umbriferella (Herrich-Schäffer, 1854)
  aurimaculella (Höfner, 1897)
  ornata (Dufrane, 1942), unavailable
Oxypteryx nigritella (Zeller, 1847) **comb. nov. [113]**
Oxypteryx immaculatella (Douglas, 1850)
  phaeella (Heckford & Langmaid, 1988)
Oxypteryx plumbella (Heinemann, 1870) **comb. nov. [113]**
Oxypteryx isostacta (Meyrick, 1926) **comb. nov. [113]**
Oxypteryx helotella (Staudinger, 1859) **comb. nov. [113]**
  damonella (Millière, 1876)
  algeriella (Baker, 1888)
  doliodes (Meyrick, 1891)
  striatopunctella (Rebel, 1891)
  levisella (Chrétien, 1922)
Oxypteryx parahelotella (Nel, 1995) **comb. nov. [113]**
Oxypteryx graecatella (Šumpich & Skyva, 2012) **comb. nov. [113]**

Gelechiinae Stainton, 1954
Gelechiini Stainton, 1954

Xystophora **Wocke, 1876**
    Doryphora Heinemann, 1870, homonym
    Doryphorella Cockerell, 1888
Xystophora carchariella (Zeller, 1839)
Xystophora pulveratella (Herrich-Schäffer, 1854)
    intaminatella (Stainton, 1860)
    steudeliella (Frey, 1880)

Athrips **Billberg, 1820 [118]**
    Rhynchopacha Staudinger, 1871
    Epithectis Meyrick, 1895
    Leobatus Walsingham, 1904
    Ziminiola Gerasimov, 1930
    Cremona Busck, 1934
Athrips spiraeae (Staudinger, 1871)
Athrips pruinosella (Lienig & Zeller, 1846)
Athrips rancidella (Herrich-Schäffer, 1854) **[119]**
    triatomaea (Mühlig, 1864)
    vepretella (Zeller, 1870)
    superfetella (Peyerimhoff, 1877)
    cotoneastri (Busck, 1934)
    haifella Amsel, 1935
    cerasivorella (Kuznetsov, 1960)
Athrips thymifoliella (Constant, 1893)
Athrips amoenella (Frey, 1882) **[120]**
    allgunnensis Svensson, 1993, unavailable
Athrips nigricostella (Duponchel, 1842)
Athrips tetrapunctella (Thunberg, 1794)
    lathyri (Stainton, 1865)
    lathyrella (Doubleday, 1866), emendation
Athrips mouffetella (Linnaeus, 1758)
    pedisequella ([Denis & Schiffermüller], 1775)
    punctifera (Haworth, 1828)
Athrips asarinella (Chrétien, 1930)
Athrips medjella (Chrétien, 1900)
Athrips patockai (Povolný, 1979)
Athrips polymaculella Park, 1991
Athrips stepposa Bidzilya, 2005
Athrips aquila Junnilainen, 2010
Athrips bidzilyai Junnilainen, 2010
Athrips fagoniae (Walsingham, 1904)

Neofriseria **Sattler, 1960**
Neofriseria peliella (Treitschke, 1835) **[121]**
　　senecionella (Bruand d´Uzelle, 1859)
Neofriseria singula (Staudinger, 1876)
　　suppeliella (Walsingham, 1896)
　　amaurella (Rebel, 1927), homonym
　　ifranella (Lucas, 1956)
　　hispanicella (Amsel, 1953)
Neofriseria pseudoterrella (Rebel, 1928)
Neofriseria baungaardiella Huemer & Karsholt, 1999
Neofriseria hitadoella Karsholt & Vives, 2014 **[122]**
Neofriseria kuznetzovae Bidzilya, 2002 **[123]**
Neofriseria caucasicella Sattler, 1960
Neofriseria mongolinella Piskunov, 1987

Prolita **Leraut, 1993**
　　Lita Treitschke, 1833, homonym
Prolita sexpunctella (Fabricius, 1794)
　　virgella (Thunberg, 1794)
　　longicornis (Curtis, 1827)
　　longicornella (Doubleday, 1859), emendation
　　histrionella (Geyer, 1832)
　　zebrella (Treitschke, 1833)
　　alpicolo (Frey, 1867)
　　alternatella (Kearfott, 1908)
　　melanica (Strand, 1920), unavailable
　　petulans (Braun, 1925)
Prolita solutella (Zeller, 1839)
　　fumosella (Douglas, 1852)
　　cornubiae (Boyd, 1858)
　　pribitzeri (Rebel, 1889)
　　nigrobipunctatella (Lucas, 1932)

Sophronia **Hübner, 1825 [124]**
Sophronia semicostella (Hübner, 1813) **[125]**
　　marginella (Thunberg, 1794), homonym
Sophronia gelidella Nordman, 1941
Sophronia consanguinella Herrich-Schäffer, 1854 **[126]**
　　marginella Toll, 1936
Sophronia illustrella (Hübner, 1796)
Sophronia grandii Hering, 1933 **[127]**
　　ascalis Gozmány, 1951, **syn. nov.**
Sophronia chilonella (Treitschke, 1833) **[128]**

Sophronia finitimella Rebel, 1905
Sophronia acaudella Rebel, 1903
Sophronia curonella Standfuss, 1884
Sophronia humerella ([Denis & Schiffermüller], 1775)
Sophronia sicariellus (Zeller, 1839) **[129]**
Sophronia santolinae Staudinger, 1863

Mirificarma Gozmány, 1955 [130]
Helina Guenée, 1849, homonym
Mirificarma rhodoptera (Mann, 1866)
Mirificarma minimella Huemer & Karsholt, 2001
Mirificarma denotata Pitkin, 1984
Mirificarma maculatella (Hübner, 1796)
Mirificarma aflavella (Amsel, 1935)
Mirificarma flavella (Duponchel, 1844)
    segetella (Zeller, 1847)
Mirificarma eburnella ([Denis & Schiffermüller], 1775)
    formosella (Hübner, 1796), homonym
    flammella (Hübner, 1825)
    rufeoformosella (Bruand d´Uzelle, 1859)
Mirificarma fasciata Pitkin, 1984
Mirificarma lentiginosella (Zeller, 1839) **[131]**
Mirificarma pederskoui Huemer & Karsholt, 1999
Mirificarma cytisella (Treitschke, 1833) **[132]**
    roseella (Hauder, 1918), unavailable
    leonella Amsel, 1959, subspecies
Mirificarma monticolella (Rebel, 1931) **[133]**
Mirificarma interrupta (Curtis, 1827)
    interuptella (Hübner, 1793), homonym
Mirificarma burdonella (Rebel, 1930) **[134]**
Mirificarma cabezella (Chrétien, 1925)
Mirificarma ulicinella (Staudinger, 1859) **[135]**
Mirificarma mulinella (Zeller, 1839)
    caminariella (Fuchs, 1902)
    nigraesilvae (Amsel, 1950)

Aroga Busck, 1914
Aroga velocella (Zeller, 1839) **[136]**
    affiniella (Zetterstedt, 1839)
    tesserella (Zetterstedt, 1839)
    brunnea (Schöyen, 1882)
    aterrimella (Rebel, 1889)
    peperistis (Meyrick, 1926)

　　rupicolella (Müller-Rutz, 1934)
Aroga flavicomella (Zeller, 1839) **[137]**
　　aureodorsella (Bruand d´Uzelle, 1859)
Aroga eatoni Corley & Goodey, 2014
Aroga pascuicola (Staudinger, 1871)
　　eremella (Chrétien, 1915)
Aroga aristotelis (Millière, 1876)
　　astragali (Staudinger, 1879)
　　fulminella (Millière, 1882)
　　lacertella (Walsingham, 1904)
　　aplasticella (Rebel, 1913), unavailable
　　hyrcanella (Toll, 1948)
Aroga corsa Varenne & Nel, 2019
Aroga temporariella Sattler, 1960
Aroga balcanicola Huemer & Karsholt, 1999

Filatima Busck, 1939
Filatima angustipennis Sattler, 1961
　　albicosta auct.
Filatima pallipalpella (Snellen, 1884)
Filatima spurcella (Duponchel, 1843)
　　fuscantella (Heinemann, 1870)
Filatima transsilvanella Kovács & Kovács, 2002
Filatima algarbiella Corley, 2014
Filatima tephritidella (Duponchel, 1844)
　　tephriditella (Herrich-Schäffer, 1854)
Filatima textorella (Chrétien, 1908)
Filatima djakovica Anikin & Piskunov, 1996
Filatima incomptella (Herrich-Schäffer, 1854)
　　turbidella (Nolcken, 1871)
Filatima ukrainica Piskunov, 1971
Filatima zagulajevi Anikin & Piskunov, 1996

Chionodes Hübner, 1825 [138]
Chionodes lugubrella (Fabricius, 1794)
　　luctificella (Hübner, 1813)
　　lunatella (Zetterstedt, 1839)
Chionodes tragicella (Heyden, 1865)
　　libidinosa (Staudinger, 1871)
Chionodes soella Huemer & Sattler, 1995
Chionodes luctuella (Hübner, 1793) **[139]**
　　sauteriella (Zeller, 1868)
Chionodes aprilella Huemer & Sattler, 1995

Chionodes violacea (Tengström, 1848)
Chionodes mongolica Piskunov, 1979
   ukrainica Piskunov, 1979
Chionodes holosericella (Herrich-Schäffer, 1854)
   cognatella (Heinemann, 1870)
   norvegiae (Strand, 1903)
   dovrella (Grønlien, 1925)
   meesi (Barca, 1932)
   danieli (Osthelder, 1951)
Chionodes praeclarella (Herrich-Schäffer, 1854)
   pergrandella (Rebel, 1917)
   colorella (Caradja, 1920), unavailable
   decolorella auct.
Chionodes caucasicella Huemer & Sattler, 1995
Chionodes nubilella (Zetterstedt, 1839)
   tarandella (Wocke, 1864)
Chionodes continuella (Zeller, 1839)
   brumella (Clemens, 1864)
   trimaculella (Packard, 1867)
   albomaculella (Chambers, 1875)
Chionodes perpetuella (Herrich-Schäffer, 1854)
Chionodes apolectella (Walsingham, 1900)
Chionodes distinctella (Zeller, 1839)
   striolatella (Heinemann, 1870)
   tristella (Teich, 1889)
   indistinctella (Rebel, 1901)
   latiorella (Amsel, 1939)
   unicolor (Toll, 1948)
   deserticola Piskunov, 1979
Chionodes hayreddini Koçak, 1986
   ochripalpella (Frey, 1880), homonym
Chionodes hinnella (Rebel, 1935)
Chionodes bastuliella (Rebel, 1931)
Chionodes electella (Zeller, 1839)
Chionodes viduella (Fabricius, 1794)
   leucomella (Quenzel, 1802)
   luctiferella (Herrich-Schäffer, 1856)
   labradoriella (Clemens, 1863)
Chionodes nebulosella (Heinemann, 1870)
Chionodes fumatella (Douglas, 1850) **[140]**
   celerella (Stainton, 1851)
   oppletella (Herrich-Schäffer, 1854)
   reuttiella (Heinemann, 1870)

nigricans (Heinemann, 1870)
syrticola (Staudinger, 1871)
brunnea (Teich, 1901), homonym
carpella Piskunov, 1971
Chionodes ignorantella (Herrich-Schäffer, 1854)
ochrisignella (Nolcken, 1871)

Gelechia Hübner, 1825 [141]
Guenea Bruand d´Uzelle, 1851
Cirrha Chambers, 1872
Oeseis Chambers, 1875
Mesogelechia Omelko, 1986
Gelechia rhombella ([Denis & Schiffermüller], 1775)
rhombea (Haworth, 1828), emendation
axilella (Thunberg, 1794)
Gelechia scotinella Herrich-Schäffer, 1854
conspurcatella Heinemann, 1870
confusella Heinemann, 1870
kiesenwetteri Heuäcker, 1873
lakatensis Rebel, 1904
baueri (Rebel, 1917)
Gelechia senticetella (Staudinger, 1859) **[142]**
limitanella Rebel, 1904
nigrostriella (Zerny, 1936)
Gelechia obscuripennis (Frey, 1880) **[143]**
melanotica (Burmann, 1950), unavailable
albicans (Burmann, 1950), unavailable
Gelechia sabinellus (Zeller, 1839)
hoffmanniella (Strand, 1902)
corsella (Rebel, 1930)
kalevalella (Kanerva, 1936)
Gelechia atlanticella (Amsel, 1955)
Gelechia nervosella (Zerny, 1927)
thuriferella (Cleu, 1936)
Gelechia sororculella (Hübner, 1817)
Gelechia jakovlevi Krulikovsky, 1905
nigrovittata Schantz, 1971
Gelechia muscosella Zeller, 1839
griseella Caradja, 1920
Gelechia cuneatella Douglas, 1852
Gelechia aspoecki Huemer, 1992
Gelechia asinella (Hübner, 1796)
aurorella Frey, 1882

Gelechia hippophaella (Schrank, 1802)
   basalis Stainton, 1854
   acupediella Frey, 1870
Gelechia basipunctella Herrich-Schäffer, 1854
   basiguttella Heinemann, 1870
   albicans Heinemann, 1870
Gelechia nigra (Haworth, 1828)
   cautella Zeller, 1839
Gelechia turpella ([Denis & Schiffermüller], 1775)
   populella (Hübner, 1796)
   nebulea (Haworth, 1828), unavailable
   pinguinella (Treitschke, 1832)
   kochiella (Herrich-Schäffer, 1854)
Gelechia rhombelliformis Staudinger, 1871
Gelechia sirotina Omelko, 1986
Gelechia sestertiella Herrich-Schäffer, 1854
Gelechia mediterranea Huemer, 1991
Gelechia dujardini Huemer, 1991

***Psoricoptera* Stainton, 1854**
Psoricoptera speciosella Teich, 1893
Psoricoptera gibbosella (Zeller, 1839)
   triorthias (Meyrick, 1935)
   lepigreella (Lucas, 1938)

***Agnippe* Chambers, 1872 [144]**
   Evippe Chambers, 1873
   Phaetusa Chambers, 1875, homonym
   Tholerostola Meyrick, 1917
Agnippe echinuloides Bidzilya & Li, 2010
Agnippe lunaki (Rebel, 1941)
   penicillata (Amsel, 1961)
Agnippe pseudolella (Christoph, 1888)
   cephalella (Caradja, 1920)

***Holcophora* Staudinger, 1871 [145]**
   Aponoaea Walsingham, 1905
Holcophora statices Staudinger, 1871
Holcophora inderskella (Caradja, 1920) **[146]**
Holcophora obtusipalpis (Walsingham, 1905)
   cinerellus (Turati, 1930)

Gnorimoschemini Povolný, 1964

***Gnorimoschema* Busck, 1900**
    Lerupsia Riedl, 1965
    Neoschema Povolný, 1967
Gnorimoschema soffneri (Riedl, 1965)
    antiquum Povolný, 1966
Gnorimoschema herbichii (Nowicki, 1864) **[147]**
    pusillella (Rebel, 1893)
    tengstroemiella (Joannis, 1910)
    pazsiczkyi (Rebel, 1913)
    parentesella (Toll, 1936)
    tengstroemi (Hackman, 1946)
    mongoliae Povolný, 1973, subspecies
    kamchaticum Povolný, 1977, subspecies
Gnorimoschema bodillum Karsholt & Nielsen, 1974
Gnorimoschema nupponeni Huemer & Karsholt, 2010
Gnorimoschema robustella (Staudinger, 1871)
    syrphetopa (Meryick, 1926)
Gnorimoschema steueri Povolný, 1975
Gnorimoschema epithymella (Staudinger, 1859)
    brunneomaculella (Hackman, 1946), subspecies
    boerneri (Amsel, 1952), subspecies
    kirgisicum Povolný, 1994, subspecies
Gnorimoschema nordlandicolella (Strand, 1902)
    cyceonodes (Meyrick, 1924)
    eucausta (Meyrick, 1929)
    fennicella (Hackman, 1946)
Gnorimoschema nilsi Huemer, 1996
Gnorimoschema valesiella (Staudinger, 1877)
    diabolicella (Hering, 1924)
    charcoti (Meyrick, 1934)
    hackmani (Schantz, 1952)
Gnorimoschema streliciella (Herrich-Schäffer, 1854)
Gnorimoschema hoefneri (Rebel, 1909)

***Scrobipalpopsis* Povolný, 1967**
Scrobipalpopsis petasitis (Pfaffenzeller, 1867)
    petasitella (Staudinger, 1867)
    petasitae (Heinemann, 1870), emendation

***Tecia* Povolný, 1973**
Tecia solanivora (Povolný, 1973)

***Scrobipalpa* Janse, 1951 [148]**
    Ilseopsis Povolný, 1965

   Euscrobipalpa Povolný, 1967
   Ergasiola Povolný, 1967
*Scrobipalpa aptatella (Walker, 1864) **[149]**
   heliopa (Lower, 1900)
Scrobipalpa kasyi Povolný, 1968
Scrobipalpa notata (Povolný, 2001)
Scrobipalpa acuminatella (Sircom, 1850)
   pulliginella (Sircom, 1850)
   cirsiella (Stainton, 1851)
   porcella (Heinemann, 1870)
   ingloriella (Heinemann, 1870)
   gracilella (Stainton, 1871)
Scrobipalpa skulei Huemer & Karsholt, 2010
Scrobipalpa hungariae (Staudinger, 1871)
Scrobipalpa adaptata (Povolný, 2001)
Scrobipalpa brahmiella (Heyden, 1862)
Scrobipalpa vasconiella (Rössler, 1877)
   drahomirae Povolný, 1966
Scrobipalpa dorsolutea Huemer & Karsholt, 2010
Scrobipalpa amseli Povolný, 1966 **[150]**
Scrobipalpa hyssopi Nel, 2003 **[150]**
Scrobipalpa montanella (Chrétien, 1910)
Scrobipalpa corleyi Huemer & Karsholt, 2010
Scrobipalpa chrysanthemella (Hofmann, 1867)
   opificella (Mann, 1878)
Scrobipalpa proclivella (Fuchs, 1886)
   rancidella auct.
Scrobipalpa frugifera Povolný, 1969
   hypothetica Povolný, 1973
Scrobipalpa oleksiyella Huemer & Karsholt, 2010
Scrobipalpa smithi Povolný & Bradley, 1964
Scrobipalpa occulta (Povolný, 2002)
   sibirica Bidzilya, 2009
Scrobipalpa grisea Povolný, 1969
   uralensis Povolný, 1973, unavailable
Scrobipalpa usingeri Povolný, 1969
Scrobipalpa clintoni Povolný, 1968
   linella Piskunov, 1975
   deleta Povolný, 1981
Scrobipalpa reiprichi Povolný, 1984 **[151]**
Scrobipalpa obsoletella (Fischer v. Röslerstamm, 1841)
   miscitatella (Clarke, 1932)
   bipunctella (Hartig, 1941)
   calaritanella (Amsel, 1952)

   hospes Povolný, 1964
Scrobipalpa feralella (Zeller, 1872)
   rebeliella (Hauder, 1917)
Scrobipalpa halonella (Herrich-Schäffer, 1854)
Scrobipalpa perinii (Klimesch, 1951)
Scrobipalpa phagnalella (Constant, 1895)
   staehelinella (Caradja, 1920), unavailable
Scrobipalpa tokari Huemer & Karsholt, 2010
Scrobipalpa karadaghi (Povolný, 2001)
Scrobipalpa heimi Huemer & Karsholt, 2010
Scrobipalpa acuta (Povolný, 2001)
Scrobipalpa soffneri Povolný, 1964
Scrobipalpa jariorum Huemer & Karsholt, 2010
Scrobipalpa murinella (Duponchel, 1843)
   culminicolella (Staudinger, 1871)
   excelsa (Frey, 1880)
Scrobipalpa wiltshirei Povolný, 1966
   obrteliana Povolný, 1971, subspecies
Scrobipalpa caucasica (Povolný, 2001) **[152]**
   bezengensis (Povolný, 2001)
Scrobipalpa pauperella (Heinemann, 1870) **[153]**
   klimeschi Povolný, 1967
Scrobipalpa spumata (Povolný, 2001)
Scrobipalpa arenbergeri Povolný, 1973
Scrobipalpa mercantourica Varenne & Nel, 2018 **[154]**
Scrobipalpa nana Povolný, 1973
   caroxyli (Falkovitsh & Bidzilya, 2006), subspecies
Scrobipalpa heretica Povolný, 1973
   submagnificella Povolný, 1977
Scrobipalpa bigoti Povolný, 1973
   tunesica Povolný, 1979, subspecies
Scrobipalpa dorsoflava (Povolný, 1996)
Scrobipalpa magnificella Povolný, 1967
Scrobipalpa abstrusa Huemer & Karsholt, 2010
Scrobipalpa superstes Povolný, 1977
Scrobipalpa remota Povolný, 1972
Scrobipalpa plesiopicta Povolný, 1969
Scrobipalpa bradleyi Povolný, 1971
   glaserorum Povolný, 1977
   meyricki auct.
Scrobipalpa selectella (Caradja, 1920)
   fraterna Povolný, 1969
Scrobipalpa alterna (Falkovitsh & Bidzilya, 2006) **[155]**

Scrobipalpa lutea Povolný, 1977 **[155]**
Scrobipalpa griseoflava Bidzilya & Budashkin, 2011
Scrobipalpa niveifacies Povolný, 1977
    milleri Povolný, 1977
Scrobipalpa indignella (Staudinger, 1879)
    pseudobsoletellum (Povolný & Gregor, 1955)
    hyoscyamivora (Gerasimov, 1940)
    grossa Povolný, 1966
Scrobipalpa punctata (Povolný, 1996)
Scrobipalpa lagodes (Meyrick, 1926)
*Scrobipalpa deluccae Povolný, 1966
Scrobipalpa atriplicella (Fischer von Röslerstamm, 1841)
    atrella (Thunberg, 1788), homonym
    detersella (Clemens, 1860), homonym
    infumatella (Fuchs, 1901)
    brackenridgiella (Busck, 1903)
    chenopodiella (Busck, 1916)
    arogantella Povolný, 1967
    altajica Povolný, 1969
Scrobipalpa suaedella (Richardson, 1893)
    flavidorsella (Amsel, 1952)
    hartigi Povolný, 1977
Scrobipalpa solitaria Povolný, 1969
*Scrobipalpa dagmaris Povolný, 1987
    rezniki Piskunov, 1990
    turkmenica Piskunov, 1990
Scrobipalpa suasella (Constant, 1895)
Scrobipalpa hendrikseni Huemer & Karsholt, 2010
Scrobipalpa halimifolia Bidzilya & Budashkin, 2011
Scrobipalpa traganella (Chrétien, 1915)
Scrobipalpa bazae Povolný, 1977
Scrobipalpa artemisiella (Treitschke, 1833) **[156]**
    ancillella (Bruand d'Uzelle, 1851)
    paniculatella (Novickij, 1924)
    mongolensis Povolný, 1969
    oreocyrniella (Petry, 1904), subspecies
    syriaca Povolný, 1967, subspecies
Scrobipalpa stangei (Hering, 1889) **[156]**
    saltenella (Meess, 1910)
Scrobipalpa suaedivorella (Chrétien, 1915)
    detersipunctella (Toll, 1947)
Scrobipalpa bryophiloides Povolný, 1966 **[157]**
Scrobipalpa algeriensis Povolný & Bradley, 1964

Scrobipalpa deutschi Huemer & Karsholt, 2010
Scrobipalpa disjectella (Staudinger, 1859)
Scrobipalpa fontanensis Varenne & Nel, 2017
Scrobipalpa mixta Huemer & Karsholt, 2010
Scrobipalpa achtubica Anikin & Piskunov, 2018
Scrobipalpa rebeli (Preissecker, 1914)
   fuscella (Klimesch, 1938)
   japonica Povolný, 1977
Scrobipalpa gallicella (Constant, 1885)
Scrobipalpa ustulatella (Staudinger, 1871)
Scrobipalpa postulatella Huemer & Karsholt, 2010
Scrobipalpa filia Povolný, 1969
Scrobipalpa nitentella (Fuchs, 1902)
   seminella (Pierce & Metcalfe, 1935)
Scrobipalpa costella (Humphreys & Westwood, 1845)
   costimaculella (Bruand d´Uzelle, 1859)
Scrobipalpa hyoscyamella (Stainton, 1869)
Scrobipalpa portosanctana (Stainton, 1859)
   eremaula (Meyrick, 1891)
   lyciella (Walsingham, 1900)
   desertella (Rebel, 1901)
   bertramella (Lucas, 1940)
   leroyella (Lucas 1950)
   reisseri (Povolný & Gregor, 1955)
   philolycii (Hering, 1957)
   gallincolella auct.
Scrobipalpa vicaria (Meyrick, 1921)
   tineiformis Povolný, 1967
Scrobipalpa ocellatella (Boyd, 1858) **[158]**
   ocellatella (Stainton, 1859), homonym
   submissella (Stainton, 1859)
   horticolella (Rössler, 1866)
   clarella (Caradja, 1920)
   obscurior (Rebel, 1927)
   orientale (Gregor & Povolný, 1954)
   portosanctana auct.
Scrobipalpa pulchra Povolný, 1967
Scrobipalpa gecko (Walsingham, 1911)
Scrobipalpa hannemanni Povolný, 1966
   furva Povolný, 1969, subspecies
   gamanthi (Falkovitsh & Bidzilya, 2006), subspecies
Scrobipalpa erichi Povolný, 1964
Scrobipalpa divisella (Rebel, 1936)

Scrobipalpa voltinella (Chrétien, 1898)
Scrobipalpa corsicamontes Varenne & Nel, 2013
Scrobipalpa suaedicola (Mabille, 1906)
    suaedicola (Amsel, 1939), homonym
    mabillei Povolný, 1971
Scrobipalpa monochromella (Constant, 1895)
Scrobipalpa samadensis (Pfaffenzeller, 1870)
    plantaginella (Stainton, 1883)
    brunhildae (Schawerda, 1921)
    zimmermanni (Zimmermann, 1923), unavailable
    mariae (Zimmermann, 1926)
    testacella (Rebel, 1935)
    echo (Meyrick, 1937)
Scrobipalpa salinella (Zeller, 1847) **[159]**
    omachella auct.
    zernyella (Rebel, 1918)
    corsicanum (Gregor & Povolný, 1954)
    ignotum (Gregor & Povolný, 1954)
    trebujenae Povolný, 1977
Scrobipalpa spergulariella (Chrétien, 1910) **[159]**
Scrobipalpa salicorniae (Hering, 1889) **[159]**
    caliacrae (Caradja, 1932)
Scrobipalpa halimioniella Huemer & Karsholt, 2010
Scrobipalpa thymelaeae (Amsel, 1939)
Scrobipalpa halymella (Millière, 1864) **[160]**
Scrobipalpa camphorosmella Nel, 1999
Scrobipalpa stabilis Povolný, 1977 **[160]**
Scrobipalpa instabilella (Douglas, 1846)
    lagunella (Chrétien, 1910)
    strobilacella (Caradja, 1920), unavailable
    salsolella (Amsel, 1935)
    halymiphaga (Amsel, 1952)
Scrobipalpa peterseni (Povolný, 1965)
Scrobipalpa ergasima (Meyrick, 1916)
    hyoscyamella (Rebel, 1912), homonym
    mignatella (Caradja, 1920), unavailable
    intestina (Meyrick, 1921)
    mirabile (Gregor & Povolný, 1955)
    pervada (Clarke, 1962)

***Turcopalpa* Povolný, 1973**
Turcopalpa glaseri Povolný, 1973

***Scrobipalpula* Povolný, 1964 [161]**
Scrobipalpula psilella (Herrich-Schäffer, 1854)
    nocturnella (Staudinger, 1859)
    pallidella (Heinemann, 1870)
    killiasii (Frey, 1880)
    astericolellum (Hering, 1957), unavailable
    asiatica Povolný, 1968, subspecies
Scrobipalpula ramosella (Müller-Rutz, 1934)
Scrobipalpula seniorum Povolný, 2000
    ptarmicae (Hering, 1957), unavailable
    compositella (Povolný, 1964), unavailable
Scrobipalpula diffluella (Frey, 1870)
    cacuminum (Frey, 1870)
    diffluella (Heinemann, 1870)
    bellidiastri (Klimesch, 1951)
    uniflorellum (Hering, 1957), unavailable
Scrobipalpula tussilaginis (Stainton, 1867)
    tussilaginella (Heinemann, 1870)
    retusella (Rebel, 1891)

***Phthorimaea* Meyrick, 1902**
Phthorimaea operculella (Zeller, 1873)
    terrella (Walker, 1864)
    solanella (Boisduval, 1874)
    tabacella (Ragonot, 1879)
    sedata (Butler, 1880)
    argentinae Povolný, 1989
    piscipellis auct.
    epicentra auct.

***Tuta* Kieffer & Jørgensen, 1910**
Tuta absoluta (Meyrick, 1917)

***Keiferia* Busck, 1939 [162]**
Keiferia lycopersicella (Walsingham, 1897)

***Ephysteris* Meyrick, 1908**
    Microcraspedus Janse, 1958
    Opacopsis Povolný, 1964
    Echinoglossa Clarke, 1965
Ephysteris promptella (Staudinger, 1859) **[163]**
    despectella (Walker, 1863)
    petiginella (Mann, 1867)

 parvula (Staudinger, 1879)
 cacomicra (Walsingham, 1908)
 chersaea Meyrick, 1908
 oschophora (Meyrick, 1910)
 crystallista (Meyrick, 1911)
 dispensata (Meyrick, 1921)
 fanatica (Meyrick, 1921)
 xanthorhabda (Gozmány, 1951)
 australiae Povolný, 1977
Ephysteris tenuisaccus Nupponen, 2010
Ephysteris deserticolella (Staudinger, 1871)
 albocapitella (Rebel, 1928)
 buvati (Povolný, 1992)
Ephysteris insulella (Heinemann, 1870)
 insularis (Staudinger, 1871)
 praticolella (Christoph, 1872), subspecies
 gallica (Povolný, 1992)
Ephysteris brachyptera Karsholt & Sattler, 1998
Ephysteris diminutella (Zeller, 1847) **[164]**
 lunaki (Hartig, 1941)
 treskensis Povolný, 1964
 hispanica Povolný, 1981
 foulonsensis Povolný, 1981
Ephysteris inustella (Zeller, 1839) **[165]**
 delminiella (Rebel, 1904)
 gredosensis (Rebel, 1935), subspecies
Ephysteris olympica Povolný, 1968
 monticola Povolný, 1981
Ephysteris iberica Povolný, 1977

Ochrodia **Povolný, 1966 [166]**
Ochrodia subdiminutella (Stainton, 1867)
 jamaicensis (Walsingham, 1897)
 bucolica (Meyrick, 1904)
 zygophyllella (Rebel, 1912)
 ericnista (Meyrick, 1914)
 ferritincta (Turner, 1919), subspecies
 ochrodeta (Meyrick, 1923)
 extorris (Meyrick, 1923)
 crocoleuca (Meyrick, 1923)
 unitella (Turati, 1930)
 tribulivora (Dumont, 1931)
 pulverea (Janse, 1950)

turgida (Janse, 1951)
pentamacula (Janse, 1958)
infallax (Gozmány, 1960)
tractatum (Gozmány, 1960)

Vladimirea **Povolný, 1967**
Distinxia Povolný, 1967
Vladimirea glebicolorella (Erschoff, 1874)
  submaculata Povolný, 1967

Microlechia **Turati, 1924**
  Hedma Dumont, 1932
  Megalocypha Janse, 1960
Microlechia rhamnifoliae (Amsel & Hering, 1931)
  rhamnifoliae (Amsel, 1935)
Microlechia chretieni Turati, 1924
  microcasis (Meyrick, 1929)
  micradelpha (Walsingham, 1900), homonym
  hyoscyamella (Amsel & Hering, 1931), homonym
  abzacella (Dumont, 1932)
  hyoscyami (Amsel, 1935)
  polioptera (Janse, 1960)
  aellographa (Janse, 1960)
Microlechia klimeschi (Povolný, 1972)
Microlechia karsholti (Nupponen, 2010)

Cosmardia **Povolný, 1965**
Cosmardia moritzella (Treitschke, 1835)
  morizella (Geyer, 1836)
  roseella (Zetterstedt, 1839)

Lutilabria **Povolný, 1965 [167]**
Lutilabria lutilabrella (Mann, 1857)
  robustella (Rebel, 1910)
  olympica Huemer, 1993, subspecies
Lutilabria volgensis Anikin & Piskunov, 1996
Lutilabria prolata Junnilainen & Nupponen, 2010

Klimeschiopsis **Povolný, 1967**
Klimeschiopsis kiningerella (Duponchel, 1843) **[168]**
  atralbella (Palm, 1947)
Klimeschiopsis discontinuella (Rebel, 1899)
Klimeschiopsis maritimaealpina Nel & Varenne, 2011

Klimeschiopsis terroris (Hartig, 1938)

***Caryocolum* Gregor & Povolný, 1954 [169]**
Caryocolum fischerella (Treitschke, 1833)
Caryocolum tischeriella (Zeller, 1839) **[170]**
Caryocolum alsinella (Zeller, 1868) **[171]**
   albifrontella (Heinemann, 1870)
   tristella (Heinemann, 1870)
   semidecandriella (Tutt, 1887)
   semidecandrella (Threlfall & Stainton, 1887)
Caryocolum viscariella (Stainton, 1855)
   crepusculella (Teich, 1889)
Caryocolum albifaciella (Heinemann, 1870)
   behenella (Constant, 1890)
Caryocolum vicinella (Douglas, 1851) **[172]**
   inflatella (Chrétien, 1901)
   albescens (Bankes, 1909), unavailable
   suffusa (Bankes, 1909), unavailable
Caryocolum bosalella (Rebel, 1936)
Caryocolum sciurella (Walsingham, 1908)
   rubidella (Chrétien, 1908)
Caryocolum amaurella (Hering, 1924) **[173]**
   viscariae (Schütze, 1926)
Caryocolum crypticum Huemer, Karsholt & Mutanen, 2014
Caryocolum tredosella Nel & Requena, 2017
Caryocolum oculatella (Thomann, 1930)
   ochraceella (Thomann, 1929), homonym
Caryocolum leucofasciatum Huemer, 1989
Caryocolum petryi (Hofmann, 1899)
   rougemonti (Rebel, 1907)
   repentella (Chrétien, 1908)
   benanderi (Hering, 1933)
Caryocolum baischi Huemer & Karsholt, 2010
Caryocolum repentis Huemer & Luquet, 1992
   repentella auct.
Caryocolum siculum Bella, 2008
Caryocolum inflativorella (Klimesch, 1938)
   xuthella (Rebel, 1941)
   census (Gozmány, 1954)
Caryocolum saginella (Zeller, 1868) **[174]**
   coussonella (Chrétien, 1908)
Caryocolum cauligenella (Schmid, 1863) **[175]**
Caryocolum trauniella (Zeller, 1868)

Caryocolum peregrinella (Herrich-Schäffer, 1854) **[176]**
    melantypella (Mann, 1877)
Caryocolum delphinatella (Constant, 1890)
    fiorii (Klimesch, 1953)
Caryocolum provinciella (Stainton, 1869)
Caryocolum mucronatella (Chrétien, 1900)
    poschiavensis (Rebel, 1936)
Caryocolum leucomelanella (Zeller, 1839) **[177]**
    gypsophilae (Stainton, 1869)
Caryocolum mazeli Huemer & Nel, 2005
Caryocolum leucothoracellum (Klimesch, 1953)
Caryocolum schleichi (Christoph, 1872) **[178]**
    syriacum Povolný, 1977
    dianthella (Chrétien, 1925), subspecies
    hackeri Derra, 1985
    improvisella (Rebel, 1936), subspecies
Caryocolum arenariella (Benander, 1937) **[178]**
Caryocolum marmorea (Haworth, 1828) **[179]**
    manniella (Zeller, 1839)
    marmorella (Doubleday, 1859), emendation
    pulchra (Wollaston, 1858), subspecies
    mediocorsa Varenne & Nel, 2013, subspecies
    marmoreum auct.
Caryocolum pullatella (Tengström, 1848) **[180]**
    pulla (Tengström, 1848)
    subtractella (Walker, 1864)
    livoniella (Teich, 1898)
    agricolaris (Meyrick, 1933)
Caryocolum stramentella (Rebel, 1935)
    emarginatum Huemer, 1988
Caryocolum hispanicum Huemer, 1988
Caryocolum confluens Huemer, 1988
Caryocolum srnkai Huemer & Karsholt, 2011
Caryocolum gallagenellum Huemer, 1989
Caryocolum fraternella (Douglas, 1851)
    intermediella (Hodgkinson, 1897)
Caryocolum klosi (Rebel, 1917) **[181]**
Caryocolum interalbicella (Herrich-Schäffer, 1854)
    quadrella (Fabricius, 1794), homonym
Caryocolum laceratella (Zeller, 1868)
    thurneri (Pinker, 1953)
Caryocolum dauphini Grange & Nel, 2012
Caryocolum blandella (Douglas, 1852) **nom. protectum [182]**
    signatella (Eversmann, 1844) **nom. oblitum**

maculea (Haworth, 1828), (*nec* Fabricius, 1794), emendation, misident.
Caryocolum blandelloides Karsholt, 1981
Caryocolum horoscopa (Meyrick, 1926) **stat. rev. [183]**
Caryocolum jaspidella (Chrétien, 1908)
Caryocolum proxima (Haworth, 1828)
   maculiferella (Douglas, 1851)
   maculivicinella (Bruand d´Uzelle, 1859)
   horticolla (Peyerimhoff, 1871)
   proximum auct.
Caryocolum blandulella (Tutt, 1887)
Caryocolum arenbergeri Huemer, 1989
Caryocolum tricolorella (Haworth, 1812)
   contigua (Haworth, 1828)
   acernella (Herrich-Schäffer, 1854)
Caryocolum fibigerium Huemer, 1988 **[184]**
Caryocolum junctella (Douglas, 1851) **[185]**
   aganocarpa (Meyrick, 1935)
Caryocolum cassella (Walker, 1864)
   melanotephrella (Erschoff, 1877)
   albifasciella (Toll, 1936)
   subvicinella (Hackman, 1946)
   falellum Piskunov, 1975
Caryocolum moehringiae (Klimesch, 1954)
Caryocolum petrophila (Preissecker, 1914)
   kemnerella (Palm, 1947)
Caryocolum huebneri (Haworth, 1828)
   hubnerella (Doubleday, 1866)
   knaggsiella (Stainton, 1866)
Caryocolum kroesmanniella (Herrich-Schäffer, 1854)
   huebneri auct.

Tila **Povolný, 1965**
Tila capsophilella (Chrétien, 1900)

Pogochaetia **Staudinger, 1879**
   Pogonochaetia Rye, 1881
   Chaetopogon Rye, 1881
Pogochaetia solitaria Staudinger, 1879
   ocymoidella (Walsingham, 1900), subspecies
   cabreretsi Povolný, 1981

Agonochaetia **Povolný, 1967**
   Sautereopsis Povolný, 1965
Agonochaetia terrestrella (Zeller, 1872) **[186]**

muestairella (Müller-Rutz, 1922)
Agonochaetia intermedia Sattler, 1968
Agonochaetia quartana Povolný, 1990

Canarischema Karsholt, 2017
Canarischema fuerteventura Karsholt, 2017

Sattleria Povolný, 1965 [187]
Sattleria melaleucella (Constant, 1865) **[188]**
   mariae (Frey, 1867), unavailable
   fusca (Burmann, 1954)
Sattleria arcuata Pitkin & Sattler, 1991
Sattleria pyrenaica (Petry, 1904) **[189]**
Sattleria taurandi Nel & Varenne, 2019
Sattleria karsholti Huemer & Hebert, 2011
Sattleria cottiella Huemer & Hebert, 2011
Sattleria marguareisi Huemer & Sattler, 1992
Sattleria izoardi Huemer & Sattler, 1992
Sattleria graiaeella Huemer & Hebert, 2011
Sattleria dolomitica Huemer, 2014
Sattleria basistrigella Huemer, 1997
Sattleria triglavica Povolný, 1987
Sattleria basistrigella Huemer, 1997
   basistrigella (Müller-Rutz, 1934), unavailable
Sattleria dinarica Huemer, 2014
Sattleria haemusi Huemer, 2014
Sattleria dzieduszyckii (Nowicki, 1864)
   tatrica (Gregor & Povolný, 1955)
Sattleria angustispina Pitkin & Sattler, 1991
Sattleria breviramus Pitkin & Sattler, 1991
Sattleria sophiae Timossi, 2014
Sattleria styriaca Pitkin & Sattler, 1991

Litini Bruand d'Uzelle 1859 [190]
   Teleiodini Piskunov, 1973
   Exoteleiini Omelko, 1999

Schneidereria Weber, 1957
Schneidereria pistaciella Weber, 1957 **[191]**

Teleiodes Sattler, 1960
   Dubitationis Omelko & Omelko, 1998
   Teleia Heinemann, 1870, homonym
Teleiodes vulgella ([Denis & Schiffermüller], 1775) **[191]**

   aspera (Haworth, 1828)
Teleiodes italica Huemer, 1992 **[192]**
   gallica Huemer, 1992
Teleiodes brevivalva Huemer, 1992 **[192]**
Teleiodes wagae (Nowicki, 1860)
   marsata Piskunov, 1973
Teleiodes saltuum (Zeller, 1878) **[193]**
   nigristrigella (Wocke, 1898)
Teleiodes kaitilai Junnilainen, 2010 **[193]**
Teleiodes luculella (Hübner, 1813) **[194]**
   subrosea (Haworth, 1828)
Teleiodes flavimaculella (Herrich-Schäffer, 1854) **[195]**
   rufipunctella (Steudel, 1882)
   dealbella (Klemensiewicz, 1902), unavailable
   herrichi (Dufrane, 1955), unavailable
Teleiodes albidorsella Huemer & Karsholt, 1999
Teleiodes albiluculella Huemer & Karsholt, 2001

Neotelphusa Janse, 1958
Neotelphusa sequax (Haworth, 1828)
   apicistrigella (Duponchel, 1843)
   sequaxella (Bruand d´Uzelle, 1859)
   sequacella (Doubleday, 1859), emendation
Neotelphusa huemeri (Nel, 1998)
   pseudocisti Leraut, 1997, unavailable
Neotelphusa traugotti (Huemer & Karsholt, 2001)
Neotelphusa cisti (Stainton, 1869)

Carpatolechia Căpuşe, 1964
   Vicina Omelko, 1999
Carpatolechia decorella (Haworth, 1812)
   humeralis (Zeller, 1839)
   lyellella (Humphreys & Westwood, 1845)
   incretella (Duponchel, 1845)
   humeralella (Bruand d´Uzelle, 1851), emendation
   marmoripennella (Bruand d´Uzelle, 1851)
   pisticella (Nowicki, 1860)
   scabra (Staudinger, 1870)
   erschoffii (Frey, 1880)
   subericolella (Caradja, 1920), unavailable
   buckwelli (Lucas, 1956)
   dumitrescui Căpuşe, 1964
Carpatolechia aenigma (Sattler, 1983)
Carpatolechia fugitivella (Zeller, 1839)

vovkella (Piskunov, 1973)
melanella (Romaniszyn, 1933), unavailable
Carpatolechia fugacella (Zeller, 1839)
nigrofasciella (Bruand d´Uzelle, 1851)
Carpatolechia minor (Kasy, 1978)
Carpatolechia filipjevi (Lvovsky & Piskunov, 1993)
Carpatolechia alburnella (Zeller, 1839)
seniculella (Eversmann, 1844)
radiella (Krulikowsky, 1909), unavailable
Carpatolechia notatella (Hübner, 1813)
euratella (Herrich-Schäffer, 1854)
oskella (Piskunov, 1973)
Carpatolechia proximella (Hübner, 1796)
peritella (Constant, 1885)
ochracella (Romaniszyn, 1933), unavailable
Carpatolechia intermediella Huemer & Karsholt, 1999
Carpatolechia epomidella (Tengström, 1869)

Pseudotelphusa Janse, 1958
Sattleria Căpuşe, 1968, homonym
Klaussattleria Căpuşe, 1968
Pseudotelphusa scalella (Scopoli, 1763) **[196]**
aleella (Fabricius, 1794)
bicolorella (Treitschke, 1832)
Pseudotelphusa istrella (Mann, 1866)
decuriella (Mann, 1872)
trifasciella (Rebel, 1916)
Pseudotelphusa occidentella Huemer & Karsholt, 1999
Pseudotelphusa paripunctella (Thunberg, 1794)
tigratella (Costa, 1834)
triparella (Zeller, 1839)
trijugella (Erschoff, 1877)
sultanella (Caradja, 1920)
griseella (Preissecker, 1931), unavailable
myricae (Gilles, 1936), unavailable
pseudowagae (Svensson, 1993), unavailable
Pseudotelphusa tessella (Linnaeus, 1758)
albinigrella ([Denis & Schiffermüller], 1775)
sturmella (Hübner, 1825)
berberidella (Hübner, 1825)
funestella (Geyer, 1832)
alboquadrella (Bruand d´Uzelle, 1859)

***Istrianis* Meyrick, 1918**
    Pseudoteleia Amsel, 1935
Istrianis myricariella (Frey, 1870)
Istrianis arenicolella (Caradja, 1920)
    amilcarella (Lucas, 1933)
Istrianis pseudomyricariella Bidzilya & Karsholt, 2015
Istrianis nilssoni Bidzilya & Karsholt, 2015
Istrianis brucinella (Mann, 1872)
Istrianis femoralis (Staudinger, 1876)
    comedonella (Staudinger, 1879)
    gravosensis (Rebel, 1937)
    angustipennis (Rebel, 1941)
    funebrella (Rebel, 1941)
    squamodorella auct.
Istrianis piskunovi Bidzilya & Karsholt, 2015

***Streyella* Janse, 1958**
Streyella canariensis (Walsingham, 1908)
Streyella anguinella (Herrich-Schäffer, 1861)
    ostentella (Zerny, 1934)

***Teleiopsis* Sattler, 1960**
Teleiopsis terebinthinella (Herrich-Schäffer, 1856)
Teleiopsis latisacculus Pitkin, 1988
Teleiopsis diffinis (Haworth, 1828) **[197]**
    dissimilella (Treitschke, 1833)
    scabidella (Zeller, 1839)
    friesella (Zetterstedt, 1839)
    diffinella (Doubleday, 1859), emendation
    groenliensis (Strand, 1920), unavailable
Teleiopsis lunariella (Walsingham, 1908)
Teleiopsis bagriotella (Duponchel, 1840) **[197]**
    elatella (Herrich-Schäffer, 1854)
Teleiopsis laetitiae Schmid, 2011 **[197]**
Teleiopsis lindae Schmid, 2011
Teleiopsis albifemorella (Hofmann, 1867) **[197]**
Teleiopsis paulheberti Huemer & Mutanen, 2012 **[197]**
Teleiopsis rosalbella (Fologne, 1862) **[197]**

***Xenolechia* Meyrick, 1895 [198]**
Xenolechia aethiops (Humphreys & Westwood, 1845)
    aterrima (Edleston, 1844)

　　aethiopella (Doubleday, 1859), emendation
　　squamulella (Peyerimhoff, 1871)
　　tristis (Staudinger, 1879)
Xenolechia lindae Huemer & Karsholt, 1999
Xenolechia pseudovulgella Huemer & Karsholt, 1999

Altenia Sattler, 1960
Altenia perspersella (Wocke, 1862)
　　empetrella (Karvonen, 1932)
Altenia scriptella (Hübner, 1796) **[199]**
Altenia elsneriella Huemer & Karsholt, 1999
Altenia mersinella (Staudinger, 1879)
　　melanostictella (Ragonot, 1895)
　　sagittella (Caradja, 1920)
　　praedicta (Meyrick, 1923)
　　tribolopis (Meyrick, 1927)
Altenia wagneriella (Rebel, 1926)
　　danilevskyi (Piskunov, 1973)
Altenia modesta (Danilevsky, 1955)

Recurvaria Haworth, 1828
　　Lita Kollar, 1832
　　Telea Stephens, 1834, homonym
　　Aphanaula Meyrick, 1895
　　Hinnebergia Spuler, 1910
Recurvaria nanella ([Denis & Schiffermüller], 1775)
　　pumilella ([Denis & Schiffermüller], 1775)
　　nana Haworth, 1828, emendation
　　crataegella Busck, 1903
　　unicolor Rebel, 1927
　　pruniella auct.
Recurvaria leucatella (Clerck, 1759)
　　leucatea Haworth, 1828, emendation
　　albocingulella (Duponchel, 1839)
Recurvaria thomeriella (Chrétien, 1901)
Recurvaria costimaculella Huemer & Karsholt, 2001

Coleotechnites Chambers, 1880
　　Evagora Clemens, 1860, homonym
　　Eidothea Chambers, 1873 (emendation and homonym)
　　Eucordylea Dietz, 1900
　　Pulicalvaria Freeman, 1963
Coleotechnites piceaella (Kearfott, 1903)

nigra (Kearfott, 1903), homonym
obscurella (Kearfott, 1907)

***Exoteleia* Wallengren, 1881**
　Paralechia Busck, 1903
　Heringia Spuler, 1910, homonym
　Heringiola Strand, 1917
Exoteleia dodecella (Linnaeus, 1758) **[200]**
　duodecimcristata (Retzius, 1783), unavailable
　punctulata (Fourcroy, 1785)
　dodecea (Haworth, 1828), emendation
　annulicornis (Stephens, 1834)
　favillaticella (Zeller, 1839)
　reussiella (Ratzeburg, 1840)
Exoteleia succinctella (Zeller, 1872)
　oribatella (Rebel, 1918)

***Stenolechia* Meyrick, 1894**
　Poecilia Heinemann, 1870, homonym
　Gibbosa Omelko, 1988
Stenolechia gemmella (Linnaeus, 1758)
　nivella (Fabricius, 1794)
　nivea (Haworth, 1828), emendation
　lepidella (Zeller, 1839)
　nigrovittella (Duponchel, 1839)

***Parastenolechia* Kanazawa, 1985**
　Origo Omelko, 1988
　Tutor Omelko, 1988
　Laris Omelko, 1988
Parastenolechia nigrinotella (Zeller, 1847)
　nigralbella (Herrich-Schäffer, 1854), unavailable

***Stenolechiodes* Elsner, 1996**
Stenolechiodes pseudogemmellus Elsner, 1996
Stenolechiodes macrolepiellus Huemer & Karsholt, 1999

***Parachronistis* Meyrick, 1925**
　Cochlevalva Omelko, 1986
　Dentivalva Omelko, 1986
Parachronistis albiceps (Zeller, 1839) **[201]**
　albicipitella (Herrich-Schäffer, 1854), emendation
　albicapitella (Doubleday, 1859), emendation

Schistophila Chrétien, 1899

Schistophila laurocistella Chrétien, 1899
    striatana (Lucas, 1937)

Unplaced genus

"*Telphusa*" *cistiflorella* (Constant, 1890) **[202]**

Comments on the checklist

Approximately 200 comments on systematic problems, taxonomic changes and particularly potential cryptic diversity, are mainly derived from molecular data and are cross-referenced in the checklist: [1] – [202].

[1]   Anacampsidae Bruand d'Uzelle, 1851 has priority over Gelechiidae Stainton 1854. The former name has hardly been used (Sattler 1973) and the use of the older synonym would threaten stability. Following Art. 23.9.3 (ICZN) the case should therefore be referred to the Commission for a ruling under the plenary power. The year of description of Anacampsidae is according to Viette (1977).

[2]   *Stomopteryx*. This genus is in need of a taxonomic revision and includes several probable cases of cryptic diversity, and equally probably cases of over-splitting.

[3]   *Stomopteryx nugatricella / S. mongolica / S. lineolella*. The taxonomy of these species is unresolved and should be checked in upcoming revisionary work. Junnilainen et al. (2010) separated *S. mongolica* and *S. lineolella* on morphological differences they observed in male genitalia but at the same time stated that European specimens of *S. mongolica* differ from typical Mongolian vouchers (Note: They did not compare *S. mongolica* from southern Russia with the externally similar *S. nugatricella* from Spain). DNA barcodes do not support species status of all these taxa which cluster with very low divergences in the same BIN. We therefore believe that taxonomic over-splitting cannot be excluded and would be a reasonable explanation for the current species concept, although barcode sharing between some taxa cannot be excluded.

[4]   *Stomopteryx deverrae*. We have barcoded only North African specimens so far, including a syntype from Algeria, and the material from Spain should be sequenced in future to prove the occurrence in Europe.

[5]   *Stomopterayx flavoclavella*. European samples from Spain slightly differ from a sequenced syntype from Morocco and cluster in a separate BIN. The suspected conspecificity will be addressed in an upcoming revision.

[6]   *Stomopteryx remissella*. This species represents an unresolved species complex. DNA barcodes show an extraordinarily high and largely geographic variation, reflected by eight different BINs and differences in phenotype. The recently described *Stomopteryx spathulella* (Nel et al. 2019) probably belongs to one of

the BINs summarized for *S. remissella*. However, the whole complex requires thorough revisionary work and a re-evaluation of available names.

[7]   *Stomopteryx flavipalpella*. A genetically variable species which clusters into three BINs without obvious geographic variation.

[8]   *Aproaerema*. Recently Aaarvik et al. (2017) synonymized the widely accepted and diverse genus *Syncopacma* with *Aproaerema*, resulting in numerous nomenclatural changes. We here propose the following new or revised combinations: *Aproaerema incognitana* (Gozmány, 1957) comb. nov., *Aproaerema cinctelloides* (Nel & Varenne, 2012) comb. nov., *Aproaerema wormiella* (Wolff, 1958) comb. nov., *Aproaerema azosterella* (Herrich-Schäffer, 1854) comb. nov., *Aproaerema montanata* (Gozmány, 1957) comb. nov., *Aproaerema cincticulella* (Bruand, 1851) comb. nov., *Aproaerema buvati* (Nel, 1995) comb. nov., *Aproaerema linella* (Chrétien, 1904) comb. nov., *Aproaerema captivella* (Herrich-Schäffer, 1854) comb. nov., *Aproaerema semicostella* (Staudinger, 1871) comb. nov., *Aproaerema steppicola* (Junnilainen, 2010) comb. nov., *Aproaerema cottienella* (Nel, 2012) comb. nov., *Aproaerema genistae* (Walsingham, 1908) comb. rev., *Aproaerema thaumalea* (Walsingham, 1905) comb. rev. The genus *Aproaerema* includes several yet unresolved DNA barcode clusters which may partly reflect cryptic diversity and therefore requires revisionary work.

[9]   *Aproaerema cinctella*. This species clusters into two weakly separated DNA barcode clusters with max. distance of 1.86%, probably reflecting intraspecific variation.

[10] *Aproaerema linella*. A unicolorous, dissected male from Montenegro largely corresponds with the lectotype figured by Nel et al. (1996) in the male genitalia. However, the original description of *A. linella* as well as bred samples from the type area characterize *S. linella* as a species with a distinct yellow-orange subterminal fascia or costal and tornal spots and a further yellow spot in the middle of the forewing. A female from northern Italy clustering in a separate BIN matches these phenotypical characters better and also largely agrees in the genitalia. However, in the absence of molecular data from the type-locality, identification of both specimens remains uncertain and we only tentatively assign the name *A. linella* to the former specimen and leave the latter as an unidentified cluster.

[11] *Aproaerema suecicella*. Two strongly divergent BINs (4.33% min. distance) show a geographic pattern and need to be tested for potential cryptic diversity.

[12] *Aproaerema karvoneni*. Three weakly separated BINs (1.61% min. distance) partially show geographic (probably intraspecific) variation.

[13] *Aproaerema anthyllidella*. The moderate DNA barcode variation with three BINs may reflect cryptic diversity, as e.g., suspected for the current synonym *A. natrixella* (Schmid pers. comm.) and some of the other five current synonyms, but has to be carefully checked with an integrative taxonomic approach.

[14] *Iwaruna*. Species in this genus share their BINs and partially overlap in DNA barcodes (*I. biguttella* and *I. klimeschi*) but differ in morphology. DNA barcodes of *I. heringi*, a species requiring taxonomic re-assessment, are unknown.

[15] *Anacampsis populella / A. blattariella*. A population from western Austria (Vorarlberg) shares its BIN with a unique specimen of *A. populella* from Finland though matching *A. blattariella* in morphology. This is most likely a case of a so far unrecognized introgression in these two species, though the weakly deviating DNA barcode may require further studies. All other sequenced specimens of both species group in separate BINs.

[16] *Anacampsis scintillella*. Two specimens from Spain cluster in a separate BIN.

[17] *Anacampsis obscurella*. Our limited data indicates geographically separated species with three BINs but requires additional revisionary work.

[18] *Mesophleps*. The genus was recently revised by Li and Sattler (2012). Two strongly deviating DNA barcode clusters (and BINs) from Spain and Greece probably represent undescribed species.

[19] *Nothris*. The sequence of species follows the revision by Karsholt and Šumpich (2015).

[20] *Nothris gregerseni*. A specimen from Sweden clusters into a unique BIN (3.83% min. distance, but probably representing only an intraspecific split).

[21] *Nothris radiata*. The yet unpublished occurrence in Europe is based on a DNA barcoded specimen from Macedonia (Šumpich in prep.).

[22] *Neofaculta ericetella*. This species shows high intraspecific DNA barcode variation and clusters into three BINs without geographic variation.

[23] *Neofaculta taigana*. The occurrence of this Asian species in Europe will be dealt with separately by Aarvik, Berggren, Karsholt and Mutanen.

[24] *Hypatima rhomboidella*. Genetically variable species clustering into three BINs without geographic variation.

[25] *Anarsia*. The genus requires revisionary work and probably includes two undescribed species from Greece and Cyprus respectively.

[26] *Anarsia bilbainella*. A unique sequence from the type-area in Spain clusters into a separate BIN (1.26% min. distance).

[27] *Dichomeris*. As currently understood, *Dichomeris* is the largest genus within the Gelechiidae. Ponomarenko (2009) lists 582 species (+ some species placed in *Acanthophila* and *Uliaria*). Due to the high external diversity, many genera were erected, especially for tropical species. Ponomarenko (2009) and Vives Moreno (2014) listed more than 80 synonyms of *Dichomeris*. Here we only consider genera relevant for the European fauna. The genus includes one probably undescribed species from Spain.

[28] *Dichomeris limbipunctellus / D. neatodes*. These two taxa, which have been regarded as conspecific, differ in phenotypy, show a different distribution pattern in the eastern (*D. neatodes*) and western Mediterranean (*D. limbipunctellus*), and cluster into two BINs. We accordingly list them as separate species and reinstate *D. neatodes* sp. rev. as a valid species.

[29] *Dichomeris juniperella*. The species splits into two strongly divergent BINs (5.26% min. distance), one widespread, and the other restricted to the southern Alps, reflecting possible cryptic diversity.

[30]   *Dichomeris rasilella*. A single DNA barcode from Russia is highly divergent from other samples and clusters into a separate BIN (6.26% min. distance).

[31]   *Acompsia*. The sequence of species follows the revision by Huemer and Karsholt (2002).

[32]   *Acompsia pyrenaeella*. The species clusters into three BINs, one shared with phenotypically compared specimens of *A. tripunctella* and *A. antirrhinella*, indicating occasional introgression.

[33]   *Acompsia antirrhinella*. Despite diagnostic morphological characters, this species shares the only known BIN with two genetically variable species, *A. pyrenaella* and *A. tripunctella*. See also comments under these species.

[34]   *Acompsia maculosella*. Sequences of specimens from the southern Alps group into a separate BIN and are also separated by reduced forewing markings, but agree in genitalia morphology and are therefore tentatively considered as *A. maculosella*. [

[35]   *Acompsia tripunctella*. A genetically highly variable species, which clusters into seven BINs, possibly reflecting cryptic diversity requiring revisionary work. One BIN is shared with *A. pyrenaeella* and *A. antirrhinella*. See also comments under these species.

[36]   *Brachmia*. A species from Greece (Crete) is probably undescribed (Berggren in prep.).

[37]   *Brachmia dimidiella*. A genetically variable species clustering into three different BINs.

[38]   *Helcystogramma lamprostoma*. Male and female genitalia match *Helcystogramma* Zeller, 1877 and the species was placed in this genus in recent papers (Agassiz and Bidzilya 2016, Bidzilya et al. 2019, Karsholt and Huemer 2017). The DNA barcode indicates the species as sister-group of the other European *Helcystogramma*.

[39]   *Pseudosophronia*. The identity of the three currently listed European species is somewhat doubtful and requires further analysis. Corley (2001) gives a clear indication that alleged diagnostic characters for *P. constanti* described by Nel (1998) in fact fall within the intraspecific variation of *S. exustellus*. Furthermore, a successfully sequenced specimen from the type-area of *P. constanti* fully agrees with *P. exustellus* from France and Spain. We therefore formally synonymize *P. constanti* with *P. exustellus* (syn. nov.).

[40]   *Pexicopia malvella*. The species splits into two BINs (4.33% min. distance) without geographic distinction and requires further analysis. The geographic variation in the forewing colour and pattern between specimens from Central Europe and South Europe is not reflected in the DNA barcode.

[41]   Apatetrini. Genera and species of this tribe are in need of revision. Several of the included taxa do not cluster together in a barcode-based NJ tree and Apatetrini sensu auct. is likely not a monophyum.

[42]   *Dactylotula kinkerella*. The species splits into two divergent clusters representing two BINs (4.49% min. distance).

[43]　*Apatetris*. The two species listed here, *A. agenjoi* and *A. mediterranella*, are based on morphology not strictly congeneric with the type of the genus (*A. mirabella* Staudinger, 1879 from Turkey) and probably also not with each other, but are left here pending forthcoming revisionary work. Similarly, two yet unidentified species which are probably undescribed are not closely related and only tentatively assigned to *Apatetris*.

[44]　*Apatetris mediterranella*. The species clusters into two geographically separate BINs (3.05% min. distance) and requires further revision.

[45]　*Catatinagma trivittellum*. The species splits into two geographically separate and strongly divergent clusters, representing two BINs (5.11% min. distance). These should be tested for potential cryptic diversity with further sampling and a comprehensive morphological analysis.

[46]　*Catatinagma kraterella*. The species does not cluster close to the type of the genus (*C. trivittellum*), instead appears closer to *Apatetris mediterranella*. It is, however, left in *Catatinagma* pending discovery of the unknown female and forthcoming revisionary work.

[47]　*Chrysoesthia*. This genus lacks generic revision. Three yet unassigned, but sequenced species, may partly belong to the insufficiently revised taxa of the European fauna.

[48]　*Chrysoesthia drurella*. This species splits into two strongly divergent BINs (3.69% min. distance) which partly overlap geographically and require careful re-assessment.

[49]　*Chrysoesthia atriplicella* / *C. gaditella* / *C. aletris*. Morphological revisionary work and additional DNA barcoding efforts are required to determine if these three names represent one or more species. *C. halymella* (Amsel, 1935) also belongs to this complex (Bidzilya et al. 2019).

[50]　*Metanarsia modesta*. The species splits into two BINs, one only known from extra-European Armenia.

[51]　*Oecocecis guyonella*. We were able to dissect both sexes from specimens provided by Christian Gibeaux. The female genitalia are rather similar to *Metanarsia*, but the male genitalia are strongly different. Therefore, and in the absence of molecular data, the systematic position is tentative and requires further revisionary work.

[52]　For a discussion of the validity of Palumbininae, see Ponomarenko (2005, 2008b) and Karsholt et al. (2013).

[53]　*Bryotropha*. The sequence of species follows the revision by Karsholt and Rutten (2005). We did not obtain DNA barcodes from the taxa listed in that publication as '*Bryotropha* species A' and '*Bryotropha* species B'.

[54]　*Bryotropha terrella*. Two deviating DNA barcodes from Austria group into a separate BIN (2.94% min. distance) and the corresponding specimens require careful re-evaluation.

[55]　*Bryotropha desertella*. A genetically variable species clustering into three BINs without geographical structure.

[56]   *Bryotropha hulli*. The species clusters into two BINs without geographical separation.

[57]   *Bryotropha affinis*. This species shares its BIN with one BIN of *B. umbrosella*.

[58]   *Bryotropha umbrosella*. The species clusters into two BINs, one shared with *B. affinis*, which differs in phenotype and genitalia morphology (Karsholt and Rutten 2005).

[59]   *Epidola*. Unrevised genus. The identity of *Epidola grisea*, described from a single male without an abdomen and collected in Sardinia (Amsel 1942) remains obscure and needs further revisionary work. We therefore do not include it in the current checklist of European Gelechiidae.

[60]   *Epidola semitica*. This species was described from a single male from Israel, but according to recently collected material it also occurs in Greece (new record for Europe, for detailed data see dataset in BOLD).

[61]   *Aristotelia*. This genus is in strong need of a generic revision and includes several probably undescribed species.

[62]   *Aristotelia decurtella*. This species genetically clusters into two BINs (2.25% min. distance) which are in need of morphological revision.

[63]   *Aristotelia ericinella*. Specimens from Sardinia cluster separately into a different BIN (2.73% min. distance) and are considered as a separate species.

[64]   *Aristotelia subdecurtella*. Two barcode clusters, grouping into different BINs that overlap in distribution.

[65]   *Aristotelia subericinella*. The species identity is based on barcoded material from the type area (eastern Austria). Several additional clusters formerly identified as *A. subericinella* probably include cryptic diversity and are in strong need of taxonomic revision. These clusters are considered as unidentified taxa in our analysis.

[66]   *Aristotelia billii*. DNA barcodes of this species are based upon the successfully sequenced holotype and prove a wide distribution from the Mediterranean to Kirgizia.

[67]   *Caulastrocecis*. The genus is in need of revision.

[68]   *Caulastrocecis furfurella / C. cryptoxena*. The former was considered as a senior synonym of *C. cryptoxena* but both are clearly divergent in DNA barcodes and represent different species (Bidzilya and Karsholt in prep.). We therefore reinstate *C. cryptoxena* sp. rev. as a valid species.

[69]   *Paranarsia*. The systematic position of this genus is not fully resolved. The genitalia somewhat resemble those of *Caulastrocesis* but DNA barcodes are distant. Here we follow Elsner et al. (1999) in placing these two genera next to each other.

[70]   *Megacraspedus*. This genus was recently revised with 27 newly described species from Europe (Huemer and Karsholt 2018). The authors recognized extraordinary intraspecific DNA barcode variation within several species, some of which might include additional cryptic diversity.

[71]   *Megacraspedus lanceolellus*. Genetically extremely variable species, which clusters into 19 BINs of mainly geographic variation, with an intraspecific DNA barcode variation of 12.5% (Huemer and Karsholt 2018).

[72] *Megacraspedus dolosellus*. Genetically extremely variable species, which clusters into 23 BINs of mainly geographic variation, with an intraspecific DNA barcode variation of 13.8% (Huemer and Karsholt 2018).

[73] *Megacraspedus spinophallus*. Two barcode clusters, representing separate BINs with records from nearby localities.

[74] *Megacraspedus binotella*. Genetically variable species, which clusters into three BINs without clear geographic separation.

[75] *Megacraspedus brachypteris*. Genetically variable species, which clusters into four BINs without clear geographic separation.

[76] *Megacraspedus andreneli*. Two barcode clusters, representing separate BINs with records from nearby localities.

[77] *Megacraspedus imparellus*. Genetically variable species, which clusters into three BINs with probable geographic separation.

[78] *Megacraspedus teriolensis*. Genetically variable species, which clusters into two geographically distinct BINs.

[79] *Dirhinosia*. Species in this genus partly share DNA barcodes (*D. cervinella* and *D. interposita*) but differ in morphology (Bidzilya and Budashkin 2015).

[80] *Psamathocrita*. The genus is in need of revision. A probably undescribed species has been studied by Tokár and Junnilainen (in litt.) and Barton (in litt.).

[81] *Ivanauskiella*. This small genus seems to be more diverse than hitherto recognized, reflected an unidentified species from Russia and Spain. Some of the species are found in association with *Limonium* which is a likely host plant of the larvae (OK unpublished). *Spatuncusella* Nel & Varenne, 2013 was recently synonymized with *Ivanauskiella* (Nel and Varenne 2017a).

[82] *Ivanauskiella occitanica*. This species was synonymized with *I. psamathias* by Nel and Varenne (2017a). However, it clearly differs in DNA barcodes and furthermore the forewing pattern and male genitalia figures in the original description show diagnostic characters which support a separate species. We therefore reinstate *I. occitanica* sp. rev. as a valid species.

[83] *Ptocheuusa*. The genus is in strong need of revision. Barcoding efforts for several validly described species failed to produce any sequences.

[84] *Ptocheuusa paupella*. The species clusters into three separate BINs without geographic separation.

[85] *Ptocheuusa inopella*. Two barcode clusters from Spain and Sweden represent three separate BINs and need to be re-examined.

[86] *Ptocheuusa cinerella*. We transfer *Recurvaria cinerella* Chrétien from Gelechiinae: Litini to Anomologinae as *Ptocheuusa cinerella* (Chrétien, 1908) comb. nov. The male genitalia are similar overall to other species of *Ptocheuusa* and seem sufficient for this new combination despite the lack of molecular data.

[87] *Amblypalpis*. The systematic position of this genus needs re-evaluation. It was recently published as new to Europe (Vives Moreno 2019).

[88] *Parapodia*. Material from the western and eastern Mediterranean cluster into two strongly divergent BINs (5.43% min. distance). Although an initial mor-

phological examination of females reveals no obvious diagnostic characters, these clusters should be tested for potential cryptic diversity by examining additional material and a widened morphological approach.

[89] *Isophrictis*. Unrevised genus, which includes cases of unresolved and apparently intraspecific DNA barcode divergence and probably some undescribed species, misidentified records or unrecognized synonymies for the European fauna. So far only six out of the twelve species in the checklist have been successfully barcoded.

[90] *Isophrictis kefersteiniellus*. Genetically highly variable species, which clusters into four BINs. A thorough evaluation of this problem is necessary.

[91] *Isophrictis anthemidella*. Genetically variable species, which clusters into three BINs. A thorough evaluation of this problem is necessary.

[92] *Metzneria*. The classic generic revision by Englert (1974) is out of date and several probably undescribed species or cases of distinct (though unresolved) splits in DNA barcodes urgently require a new revisionary work.

[93] *Metzneria neuropterella*. The species clusters into two BINs (2.89% min. distance) without geographic separation.

[94] *Metzneria aestivella*. The DNA barcode of a paratype of *Metzneria expositoi* Vives, 2001 from Spain fully agrees with that of *M. aestivella*. Also, the genitalia morphology of the two taxa is virtually identical, and we therefore consider *M. expositoi* to be a synonym of *M. aestivella* (syn. nov.).

[95] *Metzneria fulva / Metzneria torosulella*. Despite distinct diagnostic characters in phenotypic appearance and in the male genitalia, both species share barcodes.

[96] *Metzneria ehikeella*. The species clusters into two BINs (2.91% min. distance) without geographic separation.

[97] *Metzneria metzneriella*. This genetically variable species splits into four partly sympatric DNA barcode clusters, representing four BINs. A careful morphological examination of the problem is advisable.

[98] *Metzneria artificella*. Two weakly separated barcode clusters, representing geographically distinct BINs (1.46% min. distance), need to be re-examined.

[99] *Metzneria aprilella*. The species splits into three geographically separated DNA barcode clusters, representing three BINs. This possible case of cryptic diversity requires careful morphological re-examination.

[100] *Metzneria subflavella*. Two DNA barcodes referring to specimens from Spain and France respectively are strongly divergent and are considered separate species. These results are supported by genitalia morphology, with the Spanish specimen likely representing an undescribed species.

[101] *Metzneria campicolella*. *Metzneria varennei* Nel, 1997 was recently shown to be a synonym of *M. campicolella* (Nel and Varenne 2017b). The generic placement of this species is tentative.

[102] *Apodia martinii*. DNA barcodes of this species and *A. bifractella* with separate BINs (6.58% min. distance) fully support the species status for this long-disputed taxon. We therefore reinstate *A. martinii* sp. rev. as a valid species. Dif-

ferences from *A. bifractella* in morphology, biology and distribution still need to be studied in detail.

[103] *Pragmatodes*. This genus, which has until now been placed in Gelechiini, has always been considered monotypic and endemic to the Canary Islands. However, a group of closely related species placed under *Monochroa*, i.e., *Pragmatodes melagonella* (Constant, 1895) comb. nov., *Pragmatodes albagonella* (Varenne & Nel, 2010) comb. nov., *Pragmatodes cyrneogonlla* (Nel & Varenne, 2012) comb. nov. and *Pragmatodes parvulata* (Gozmány, 1953) comb. nov., have similar genitalia which do not fit well with *Monochroa*, and their DNA barcodes cluster separately from that genus. Moreover, the known larvae of the above-mentioned species, as well as the type species of the genus (*P. fruticosella*) all feed on plants in the family Rubiaceae, an unusual feeding substrate for Gelechiidae. The genus includes additional, probably undescribed, species from South-East Europe and the Middle East.

[104] *Pragmatodes melagonella*. Specimens initially identified as this species from France and Bulgaria differ in the DNA barcode and also morphology and are considered as separate species. The type locality of *P. melagonella* is in France.

[105] *Monochroa*. This genus is in strong need of a generic revision and includes several probably undescribed species.

[106] *Monochroa rumicetella*. Two weakly separated BINs (2.12% min. distance) without geographic separation most probably reflect intraspecific variation.

[107] *Monochroa sepicolella / M. rectifasciella*. Elsner et al. (1999) had previously discussed a two-species hypothesis which is now fully supported by two strongly divergent DNA barcode clusters representing two BINs (6.7% min. distance). *M. sepicolella* occurs in North and Central Europe, whereas the name *Monochroa rectifasciella* (Fuchs, 1902) is currently used for the species with a more southern distribution (e.g., Pastorális et al. 2013). However, this problem is in need of a thorough revisionary work taking into account all available names for both species.

[108] *Monochroa tenebrella*. Two weakly separated BINs (1.12% min. distance) without geographic separation most probably reflect intraspecific variation.

[109] *Monochroa servella*. Two BINs (2.89% min. distance) without geographic separation most probably reflect intraspecific variation.

[110] *Monochroa lucidella*. Despite a low intraspecific divergence, this species may include cryptic diversity as indicated by the morphologically and genetically (only short sequences available) weakly deviating subspecies *immaculatella* from Northern Italy.

[111] *Monochroa arundinetella / M. suffusella*. These two morphologically separate species represent one of the few cases of barcode sharing among European Gelechiidae. The author and year of description of *M. arundinetella* follow Sattler (2009).

[112] *Monochroa nomadella*. This genetically highly variable species clusters in four different and geographically separate BINs and is in strong need of revisionary

work. Junnilainen et al. (2010) recognized differences in the female genitalia between specimens collected in the Ural Mountains, Central Europe, and those figured by Elsner et al. (1999). They speculated that either material from Czechia was misidentified or that it could point to cryptic diversity. Unlike the few known females from Central Europe, specimens from South Russia are slightly brachypterous which might be a further indication of a potential species complex.

[113] *Oxypteryx. Eulamprotes* Bradley, 1971 with the type species *E. atrella* is shown to be a synonym of *Oxypteryx* Rebel, 1911 (Bidzilya et al. 2019), resulting in a number of new nomenclatural changes. We here propose the following new combinations: *Oxypteryx nigromaculella* (Millière, 1872) comb. nov., *Oxypteryx wilkella* (Linnaeus, 1758) comb. nov., *Oxypteryx ochricapilla* (Rebel, 1903) comb. nov., *Oxypteryx superbella* (Zeller, 1839) comb. nov., *Oxypteryx mirusella* Huemer & Karsholt, 2013 comb. nov., *Oxypteryx occidentella* Huemer & Karsholt, 2011 comb. nov., *Oxypteryx libertinella* (Zeller, 1872) comb. nov., *Oxypteryx baldizzonei* Karsholt & Huemer, 2013 comb. nov., *Oxypteryx gemerensis* Elsner, 2013 comb. nov., *Oxypteryx deserta* (Piskunov, 1990) comb. nov., *Oxypteryx unicolorella* (Duponchel, 1843) comb. nov., *Oxypteryx nigritella* (Zeller, 1847) comb. nov., *Oxypteryx plumbella* (Heinemann, 1870) comb. nov., *Oxypteryx isostacta* (Meyrick, 1926) comb. nov., *Oxypteryx helotella* (Staudinger, 1859) comb. nov., *Oxypteryx parahelotella* Nel, 1995 comb. nov., *Oxypteryx graecatella* Šumpich & Skyva, 2012 comb. nov. Despite this new taxonomic approach, the genus is in strong need of revision. DNA barcodes separate into three clades seemingly supported by some morphological characters. For example, species formerly considered to be in the *E. wilkella*-group and characterized by the blackish ground colour of the forewings with silvery or whitish markings, form a separate clade. Further, the genus has an extraordinary intraspecific barcode variation with 18 sequenced species belonging to 27 BINs, with at least three yet unidentified species.

[114] *Oxypteryx nigromaculella.* A specimen from Greece clusters into a separate BIN and may represent a different species.

[115] *Oxypteryx wilkella.* Two specimens from Italy and Hungary respectively are strongly divergent from the large bulk of *E. wilkella* DNA barcodes and cluster into a separate BIN. The taxonomic status of this cluster requires careful evaluation.

[116] *Oxypteryx baldizzonei.* Two strongly divergent DNA barcode clusters, representing three BINs, have been considered as intraspecific variation by Huemer et al. (2013).

[117] *Oxypteryx libertinella.* The geographic variation of DNA barcode clusters in this genetically highly variable species with eight BINs has been discussed by Huemer et al. (2013). Currently this variation is considered as an intraspecific divergence.

[118] *Athrips.* The sequence of species follows the generic revision by Bidzilya (2005).

[119] *Athrips rancidella*. A specimen from Greece clusters separately into a second BIN (2.86% min. distance) and is in need of taxonomic re-evaluation.

[120] *Athrips amoenella*. A genetically highly variable species, which clusters into five BINs.

[121] *Neofriseria peliella*. Two weakly separated BINs (1.44% min. distance) without clear geographical separation most probably reflect intraspecific variation.

[122] *Neofriseria hitadoella*. A strongly divergent BIN from France with 3.85% min. distance to *N. hitadoella* from Morocco is considered as a probable cryptic species, but the problem needs to be carefully revised.

[123] *Neofriseria kuznetzovae*. This species was listed by Piskunov (1987) and partially by Huemer and Karsholt (1999) under the name of *N. caucasicella* Sattler, 1960. The latter occurs only in the Caucasus and has not been found elsewhere in Europe.

[124] *Sophronia*. Unrevised genus with some doubtful taxa lacking DNA barcodes.

[125] *Sophronia semicostella*. Two DNA barcode clusters, grouped into two BINs, show no clear geographic separation.

[126] *Sophronia consanguinella*. *S. marginella* was recently shown to be a junior synonym of this species (Šumpich et al. 2019).

[127] *Sophronia grandii*. The DNA barcode of a paratype of *Sophronia ascalis* Gozmány, 1951 fully agrees with that of *S. grandii*. The two taxa are virtually identical, and we therefore consider *S. ascalis* to be a synonym of *S. grandii* (syn. nov.).

[128] *Sophronia chilonella*. A single DNA barcode from Bulgaria of a specimen similar to *S. chilonella* strongly deviates and may represent the taxonomically disputed and unrevised *S. acaudella*.

[129] *Sophronia sicariellus*. A single DNA barcode sequence of 504bp from Germany strongly deviates, although it may represent intraspecific variation.

[130] *Mirificarma*. Several species show a high genetic variation which could indicate cryptic diversity. Therefore, despite available taxonomic revisions by Pitkin (1984) and Huemer and Karsholt (1999), a re-evaluation of morphology seems advisable in some species.

[131] *Mirificarma lentiginosella*. Two DNA barcode clusters, which separate into two BINs (1.7% min. distance) without geographic separation.

[132] *Mirificarma cytisella*. A genetically variable species, separated into four BINs without geographic separation.

[133] *Mirificarma monticolella*. Two DNA barcode clusters from Italy and Bulgaria are highly divergent and separate into two BINs (4.49% min. distance).

[134] *Mirificarma burdonella*. Two DNA barcodes from France show a deep split into two BINs (5.78% min. distance) and require taxonomic re-evaluation.

[135] *Mirificarma ulicinella*. Two DNA barcode clusters from France and Portugal are highly divergent and separate into two BINs (3.37% min. distance).

[136] *Aroga velocella*. The species splits into three BINs, which show no clear geographic separation. The attribution of authorship follows Joannis (1922).

[137] *Aroga flavicomella*. A genetically variable species, which splits into four BINs.

[138] *Chionodes*. The sequence of species follows the revision by Huemer and Sattler (1995).

[139] *Chionodes luctuella*. DNA barcodes from central and northern Europe cluster into separate BINs (1.87% min. distance) which are currently not confirmed by morphology.

[140] *Chionodes fumatella*. DNA barcodes from central and northern Europe cluster into three geographically partially separated BINs and need taxonomic re-assessment.

[141] *Gelechia*. This genus includes at least one additional and probably undescribed species.

[142] *Gelechia senticetella*. DNA barcodes cluster into two geographically separate BINs with min. distances > 2% to the Nearest Neighbour, and need taxonomic re-assessment.

[143] *Gelechia obscuripennis*. This disputed taxon has recently been re-considered to be a separate species based on molecular data, morphology and biology (Huemer 2019).

[144] *Agnippe*. The genus (as *Evippe* Chambers, 1873) has traditionally been placed in the Litini. DNA barcodes of two species are not supportive of the systematic position of the genus in that tribe. We therefore follow Bidzilya and Li (2010) and Metz et al. (2019) in placing *Agnippe* as an isolated genus within the Gelechiini.

[145] *Holcophora*. The genera *Holocophora* and *Aponoaea* have been synonymized recently by Adamski and Sattler (2019), based on some similarities of the type-species. However, the systematic position within the Gelechiidae remains uncertain for the time being.

[146] *Holcophora inderskella*. The species was included in *Holcophora* by Adamski and Sattler (2019). It was described from Lake Indersky in Western Kazakhstan and is here attached to the European fauna despite a distance of ca. 10 km from the type-locality to the widely accepted natural border of the Continent, the Ural River.

[147] *Gnorimoschema herbichii*. Northern European populations of this species cluster into two BINs.

[148] *Scrobipalpa*. This extraordinary diverse genus still requires some taxonomic re-assessment, reflected by several yet unidentified barcode clusters which at least partly belong to undescribed species.

[149] *Scrobipalpa aptatella*. Records from Europe (France, Italy, former Yugoslavia) are unconfirmed (Huemer and Karsholt 2010).

[150] *Scrobipalpa amseli / S. hyssopi*. Both species clusters into the same BIN but differ in morphology of the male genitalia (Huemer and Karsholt 2010). Additional material should be checked to confirm if the holotype of *S. hyssopi* represents a specimen of *S. amseli* with deformed genitalia.

[151] *Scrobipalpa reiprichi*. Two geographically separate barcodes BINs (2.57% min distance) may reflect cryptic diversity, with altogether four potential species from preliminary morphological analysis (Wiesmair et al. 2018).

[152]   *Scrobipalpa caucasica.* Only known from the Caucasus. *S. benzengensis* (Povolný, 2001) is a junior synonym (Huemer and Karsholt 2010).

[153]   *Scrobipalpa pauperella.* Some externally different specimens from northern Italy are slightly divergent in their DNA barcodes and may belong to a separate species.

[154]   *Scrobipalpa mercantourica.* This species clusters together with *Scrobipalpa arenbergeri* but according to the original description differs in morphology. A taxonomic re-assessment seems advisable to fix the status of the taxon.

[155]   *Scrobipalpa alterna / S. lutea.* Both species share barcodes and are virtually indistinguishable in genitalia characters, although the ground colour of the forewings is usually distinct with rare intermediates. A re-assessment of this group is in preparation (Bidzilya in litt.).

[156]   *Scrobipalpa artemisiella / Scrobipalpa stangei.* These two species are clearly separated by their biology and female genitalia morphology, but share one barcode BIN. A second BIN of *S. artemisiella* based on a single sequence most probably reflects intraspecific variation.

[157]   *Scrobipalpa bryophiloides.* A genetically variable species which clusters into two separate BINs and requires further evaluation.

[158]   *Scrobipalpa ocellatella.* DNA barcodes of this species clusters into two weakly separated BINs (1.44% min distance), most probably reflecting intraspecific variation.

[159]   *Scrobipalpa salinella / S. salicorniae / S. spergulariella.* Although these species show diagnostic morphology (Huemer and Karsholt 2010) and (two) unique DNA barcode haplotypes, they cluster into the same BIN. The third species, viz. *S. spergulariella*, has not yet been barcoded.

[160]   *Scrobipalpa halymella / S. stabilis.* Both species cluster into the same BIN but differ weakly in morphology (Huemer and Karsholt 2010).

[161]   *Scrobipalpula.* All five successfully sequenced species share BINs, but still show species-specific DNA barcode haplotypes.

[162]   *Keiferia lycopersicella.* An American species introduced to Europe in 2008 which apparently has not established permanent populations (Huemer and Karsholt 2010).

[163]   *Ephysteris promptella.* A genetically highly variable species clustering into four BINs. A taxonomic re-evaluation of this problem is necessary.

[164]   *Ephysteris diminutella.* Two strongly divergent and geographically separate DNA barcode clusters reflected by two BINs (5.94% min. distance) require taxonomic revision.

[165]   *Ephysteris inustella.* The year of description follows Sattler (2011). The different interpretation by Huemer & Karsholt (2019) with *inustella* originally published in synonymy and only made available in 1847 is contradicted by the Code, Article 11.6.1. "However, if such a name published as a junior synonym had been treated before 1961 as an available name and either adopted as the name of a taxon or treated as a senior homonym, it is made available thereby but dates from its first publication as a synonym."

[166]   *Ochrodia.* An unidentified species from Greece (Crete) clusters with specimens from Saudia Arabia. The genus is in need of revision.

[167] *Lutilabria lutilabrella*. DNA barcodes from Slovenia and Slovakia cluster into separate BINs (3.41% min. distance) and need revisionary work.

[168] *Klimeschiopsis kiningerella*. Specimens from northern Italy cluster into a BIN separate from all other samples from various parts of Europe.

[169] *Caryocolum*. Despite extensive past revisionary work on this genus, it still includes a remarkable amount of unresolved taxonomic problems with several potential cryptic species.

[170] *Caryocolum tischeriella*. DNA barcodes cluster into three BINs without geographic separation.

[171] *Caryocolum alsinella*. A genetically highly variable species with strongly divergent DNA barcode clusters separated into three BINs. A thorough taxonomic re-assessment seems necessary.

[172] *Caryocolum vicinella*. DNA barcodes cluster into four BINs. A thorough taxonomic re-assessment seems necessary.

[173] *Carayocolum amaurella*. This genetically highly variable species clusters into five BINs, but alleged cryptic diversity is not supported by morphology (Huemer et al. 2014).

[174] *Caryocolum saginella*. DNA barcode sequences with two BINs (5.46% min. distance). clearly support the existence of a separate species in the SW-Alps (Huemer in prep.).

[175] *Caryocolum cauligenella*. A single specimen from Spain strongly deviates in DNA barcode with a separate BIN and *C. saginella* instead of *C. cauligenella* as Nearest Neighbor (5.46% min. distance). However, the specimen clearly matches the latter in phenotypy and needs taxonomic re-assessment.

[176] *Caryocolum peregrinella*. This species splits into three highly divergent allopatric clusters which most probably represent different species (Huemer in prep.). One of the major problems in resolving the taxonomic mismatches is the status of the holotype of *C. peregrinella*, a female without an abdomen and unknown type-locality, stated as Europe (Huemer 1988).

[177] *Caryocolum leucomelanella*. Two DNA barcode clusters with separate BINs (2.73% min. distance) show no geographic pattern.

[178] *Caryocolum schleichi / C. arenariella*. Initially described as different species, the largely allopatric taxa of this group have been merged into a single species by Huemer (1988). However, all these taxa are separated phenotypically and by characters in the male genitalia. As a consequence, Aarvik et al. (2017) give species status to the northern European population and re-introduced it as *C. arenariella*. Following an initial genetic analysis of the group (Huemer et al. 2014) this taxonomic change seems well supported, however, *C. schleichi* as currently understood includes several separate species. The problem is presently under revision (Huemer in prep.).

[179] *Caryocolum marmorea* spp. *mediocorsa* agrees in DNA barcode with the nominotypical subspecies.

[180] *Caryocolum pullatella*. This species shows an extraordinary genetic variation across its holarctic range (Mutanen et al. 2012) and is in strong need of taxo-

nomic re-assessment. In Europe two geographically separated DNA barcode clusters with separate BINs are present.

[181] *Caryocolum klosi*. A single DNA barcode from the French Pyrenees is highly divergent with a separate BIN (4.17% min. distance) and may represent a different species.

[182] *Caryocolum blandella*. *Lita signatella* was described from an unstated number of specimens from Kazan in Russia ("provincia Casanensi") (Eversmann 1844). The short description is insufficient for identifying the species. The type series in the Zoological Institute in St. Petersburg is apparently mixed. During earlier visits Klaus Sattler (in litt.) and OK examined alleged syntypes of *L. signatella* incorporated under that name and which proved conspecific with *Carpatolechia proximella* (Hübner), and thus *L. signatella* was formally synonymized with that species in the Russian checklist (Ponomarenko 2008). However, only a single specimen of *L. signatella* was mentioned in an earlier work on the collection of Eversmann (Bremer 1870) and this specimen was recently designated as the lectotype (Sinev et al. 2017). It is conspecific with *Caryocolum blandella* (Douglas) which thereby became a junior synonym of *L. signatella*. Whereas the name *Caryocolum blandella* has been universally in use for a widespread European species since Kloet and Hincks (1972), *Lita signatella* has to our knowledge not been used as a valid name since 1899, and it is not listed in the main catalogues of the Gelechiidae (Rebel 1901, Meyrick 1925, Gaede 1937). According to Articles 23.9.1 and 23.9.2 of the International Code of Zoological Nomenclature (ICZN 1999), we therefore declare the name *Caryocolum blandella* Douglas, 1852 to be a nomen protectum, and the name *Lita signatella* Eversmann, 1844, which has not been used as a valid name after 1899, to be a nomen oblitum. Supplementary material 1 lists 35 references by more than ten different authors that have used *C. blandella* (or its alternative spelling *C. blandellum*) in the last 50 years (ICZN article 23.9.1.2). The name is moreover used in several other published works and on numerous internet sites.

[183] *Caryocolum horoscopa*. Initially described as a species, this taxon was recently considered to be a subspecies of *Caryocolum blandella* (Huemer and Karsholt 2010). However, in addition to diagnostic morphology, DNA barcodes also clearly support a separate species status for this taxon, and we therefore reinstate *C. horoscopa* stat. rev.

[184] *Caryocolum fibigerium*. Huemer et al. (2014) had indicated likely taxonomical problems in this group highlighted by three DNA barcode clusters on the Iberian, Italian and Balkan peninsulas. These genetic splits are also supported by morphological traits and probably reflect three different species (Huemer in prep.).

[185] *Caryocolum junctella*. Two barcode clusters with separate BINs show no clear geographic separation.

[186] *Agonochaetia terrestrella*. Specimens from Switzerland and Romania cluster into a separate BIN, but are considered as conspecific (Huemer and Karsholt 2010).

[187] *Sattleria*. The sequence of species follows Huemer and Timossi (2014).

[188] *Sattleria melaleucella*. The species shares BINs with one cluster of the morphologically different *S. pyrenaica*, indicating occasional introgression.

[189] *Sattleria pyrenaica*. A genetically variable species with five different BINs, one shared with *Sattleria melaleucella*. The species requires taxonomic re-assessment.

[190] Litini. Ponomarenko (2005, 2008) showed that Teleiodini is a junior synonym of Litini, described as Litidae by Bruand d'Uzelle (1859).

[191] *Schneidereria pistaciella* Weber, 1957. The systematic placement of this genus and species follows Huemer and Karsholt (2001).

[192] *Teleiodes vulgella / T. italica / T. brevivalva*. These three species differ strongly in the male genitalia but share DNA barcodes.

[193] *Teleiodes saltuum / T. kaitilai*. Both species are closely related, mainly differing in the structures of the female genitalia. In DNA barcodes *T. saltuum* clusters into two BINs and *T. kaitilai* in a separate BIN.

[194] *Teleiodes luculella*. A genetically variable species, which clusters into three BINs. A thorough evaluation of this problem is necessary.

[195] *Teleiodes flavimaculella*. A genetically highly variable species, which clusters into three BINs. A re-evaluation of this problem is necessary.

[196] *Pseudotelphusa tessella*. Two weakly separated BINs (1.61% min. distance) without clear geographic separation are considered as intraspecific variation.

[197] *Teleiopsis diffinis / T. bagriotella / T. albifemorella / T. paulheberti / T. rosalbella*. These closely related species differ in morphology whereas barcodes give a more complex pattern. Genetic differences are generally weak with partial BIN sharing (i.e., *T. rosalbella / T. albifemorella*) and/or likely introgression in some taxa, while high intraspecific variation - with two BINs in three species - indicates possible further cryptic diversity.

[198] *Xenolechia*. Species in this genus share DNA barcodes but differ in morphology (Huemer and Karsholt 1999).

[199] *Altenia scriptella*. Two BINs without clear geographic separation are considered as intraspecific variation.

[200] *Exoteleia dodecella*. The taxonomy of dark specimens in this group, mainly observed in Central Europe, is disputed, though usually these are considered as infrasubspecific variation (Huemer and Karsholt 1999). We were able to sequence large series of specimens across Europe and discovered that DNA barcodes of normal and dark specimens are usually separated by a low but constant barcode gap of about 1%. These results, in combination with differences in adult morphology, clearly indicate presence of two separate species. Revisionary work is currently under preparation (Huemer et al. in prep.).

[201] *Parachronistis albiceps*. Genetically variable species, which clusters into four BINs without clear geographic separation.

[202] "*Telphusa*". The placement of *cistiflorella* Constant, 1890 in the genus *Telphusa* follows Sattler (1985), who pointed out that this placement should be regarded as tentative. The DNA barcode of *T. cistiflorella* clusters among genera placed in the Gelechiini, and the male genitalia are overall similar to those of *Mirificarma*, although they have no filament.

Acknowledgments

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Supplementary material 1

Selected references that have used the name *Caryocolum blandella* in the last 50 years
Authors: Peter Huemer, Ole Karsholt
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DNA barcode library for European Gelechiidae (Lepidoptera) suggests greatly underestimated species diversity

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Abstract

For the first time, a nearly complete barcode library for European Gelechiidae is provided. DNA barcode sequences (COI gene – cytochrome *c* oxidase 1) from 751 out of 865 nominal species, belonging to 105 genera, were successfully recovered. A total of 741 species represented by specimens with sequences ≥ 500bp and an additional ten species represented by specimens with shorter sequences were used to produce 53 NJ trees. Intraspecific barcode divergence averaged only 0.54% whereas distance to the Nearest-Neighbour species averaged 5.58%. Of these, 710 species possessed unique DNA barcodes, but 31 species could not be reliably discriminated because of barcode sharing or partial barcode overlap. Species

discrimination based on the Barcode Index System (BIN) was successful for 668 out of 723 species which clustered from minimum one to maximum 22 unique BINs. Fifty-five species shared a BIN with up to four species and identification from DNA barcode data is uncertain. Finally, 65 clusters with a unique BIN remained unidentified to species level. These putative taxa, as well as 114 nominal species with more than one BIN, suggest the presence of considerable cryptic diversity, cases which should be examined in future revisionary studies.

Introduction

The megadiverse family, Gelechiidae, includes approximately 4,700 known species and perhaps a similar number of undescribed taxa (Karsholt et al. 2013). With a remarkable 865 species reported from Europe and adjacent islands (Huemer and Karsholt 2020), the Gelechiidae are the fourth most diverse family of Lepidoptera after the Noctuidae, Geometridae, and Tortricidae in Europe. Due to their general dull-coloured and inconspicuously patterned wings (Fig. 1), and frequently small size, the Gelechiidae have received little attention from lepidopterists, leading to considerable gaps in knowledge of their taxonomy, systematics, biology, and distribution. In particular, the lack of generic revisions in several diverse groups has created the widespread impression of a "difficult" family which has acted to further limit interest in this group.

Over the last two decades, the Gelechiidae have received increasing attention as a result of two monographs that treated approximately half the known European species (Huemer and Karsholt 1999, 2010) and another on the Central European fauna (Elsner et al. 1999). Unfortunately, these publications, as well as several subsequent revisions (i.e., Bidzilya 2005a, 2005b, Bidzilya and Karsholt 2015, Karsholt and Rutten 2005, Karsholt and Šumpich 2015, Li and Sattler 2012), did not take advantage of new molecular methods, in particular DNA barcoding. On the contrary phylogenetic analysis of higher taxa in Gelechiidae benefitted greatly from molecular analysis (Kaila et al. 2011, Karsholt et al. 2013). However, recent studies on several genera of European Gelechiidae (Huemer et al. 2013, 2014, Huemer and Mutanen 2012, Huemer and Karsholt 2014, Landry et al. 2017) revealed the power of this approach to aid species delimitation in taxonomically difficult groups, even those with a high level of unrecorded species and cryptic diversity. Similar patterns have been analyzed in several other Lepidoptera in different parts of the world, e.g., in another gelechioid group (Mutanen et al. 2011), in Iberian butterflies (Dincă et al. 2015), in North American Noctuoidea (Zahiri et al. 2017), or in the Lepidoptera fauna of Costa Rica (Janzen and Hallwachs 2016). These results motivated the present effort to compile a comprehensive DNA barcode library for the European Gelechiidae fauna, with the aim of simplifying future revisionary studies while also improving their quality.

Figure 1. *Megacraspedus teriolensis* is a characteristic example of gelechiid moths only recognised and described during the last few years.

Materials and methods

Checklist of European Gelechiidae

The lack of an updated checklist for European Gelechiidae (see Karsholt 2004-2019) was such a major impediment to the present study that it necessitated the assembly of a new systematic list (Huemer and Karsholt 2020). This list, which includes 865 species of Gelechiidae in 109 genera, provided the basis for selecting the specimens that were analysed in this study.

Sample material

One major challenge was the difficulty in accessing specimens suitable for molecular analysis, reflecting the rarity of many species. In addition, DNA quality of the specimens was another very important limitation as sequence recovery from older specimens of rare taxa was either partial or failed completely even with protocols that employed high-throughput sequencers to analyze short amplicons. In some cases, efforts were made to recollect taxa that lacked a sequence record.

Voucher material was obtained from Europe (Fig. 2) except for eleven taxa whose sequences could not be recovered from specimens from this continent or where it
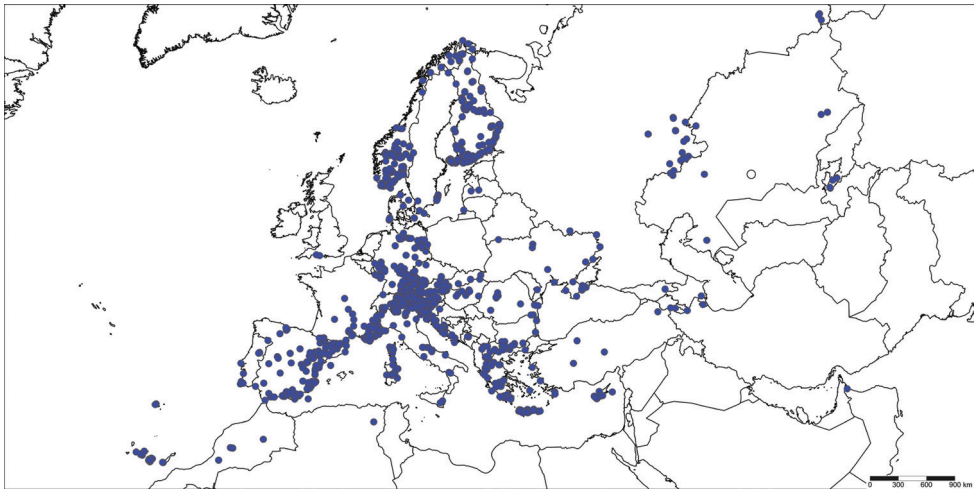
Figure 2. Distribution map of examined material of Gelechiidae (extra-European material partially mapped). SimpleMappr (http://www.simplemappr.net).

seemed important to analyze specimens to clarify taxonomy (e.g., extra-European type-material) (Suppl. material 2, 3). Approximately two-thirds of specimens originated from four nations - Germany (1319), Austria (1157), Italy (906), and Finland (707). The remaining specimens derived from 33 other countries (Fig. 2).

Many institutions and private collectors contributed to the dataset (see below), supplemented by DNA barcodes from earlier studies.

Abbreviations of private and institutional collections

BIOUG   Centre for Biodiversity Genomics, Guelph, Canada
INDO   Inatura, Dornbirn, Austria
LMK   Landesmuseum Kärnten, Klagenfurt, Austria
MFSN   Museo Friulano di Storia Natural, Udine, Italy
MZH   Finnish Museum of Natural History, Helsinki, Finland
NHM   Natural History Museum, London, United Kingdom
NHMO   Natural History Museum, University of Oslo, Oslo, Norway
NHMW   Naturhistorisches Museum, Vienna, Austria
NMPC   National Museum Prague, Czech Republic
NMS   Naturmuseum Südtirol, Bozen, Italy
RCAH   Research Collection Alfred Haslberger, Teisendorf, Germany
RCER   Research Collection Emily Requena Miret, Gurb, Spain
RCGB   Research Collection Giorgio Baldizzone, Asti, Italy
RCGT   Research Collection Giovanni Timossi, Oderzo, Italy
RCHW   Research Collection Hartmut Wegner, Adendorf, Germany
RCIB   Research Collection Ian Barton, Cambs, United Kingdom

RCIR	Research Collection Ignác Richter, Malá Čausa, Slovakia
RCJD	Research Collection Jordi Dantart, Barcelona, Spain
RCJJ	Research Collection Jari Junnilainen, Vantaa, Finland
RCJK	Research Collection Jari-Pekka Kaitila, Vantaa, Finland
RCJL	Research Collection Gérard Labonne, Montpellier, France
RCJN	Research Collection Jacques Nel, La Ciotat, France
RCJS	Research Collection Jan Skyva, Prague, Czech Republic
RCJSC	Research Collection Jürg Schmid, Illanz, Switzerland
RCKB	Research Collection Kai Berggren, Kristiansand, Norway
RCKN	Research Collection Kari and Timo Nupponen, Espoo, Finland
RCMC	Research Collection Martin Corley, Faringdon, U.K.
RCOB	Research Collection Oleksiy Bidzilya, Kiev, Ukraine
RCOR	Research Collection Oliver Rist, Vienna, Austria
RCPB	Research Collection Peter Buchner, Schwarzau am Steinfeld, Austria
RCPL	Research Collection Peter Lichtmannecker, Adlkofen, Germany
RCRH	Research Collection Robert Heckford, Plympton, Plymouth, U.K.
RCRHE	Research Collection Richard Heindel, Günzburg, Germany
RCSP	Research Collection Serge Peslier, Perpignan, France
RCTG	Research Collection Thomas Guggemoos, Ohlstadt, Germany
RCTM	Research Collection Toni Mayr, Feldkirch, Austria
RCTV	Research Collection Thierry Varenne, Nice, France
RCWS	Research Collection Wolfgang Stark, Trübensee, Austria
RCZT	Research Collection Zdenko Tokár, Šaľa, Slovakia
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
USNM	Smithsonian Institution, National Museum of Natural History, Washington DC, U.S.A.
ZMAK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
ZMKU	Taras Shevchenko National University of Kiev, Kiev, Ukraine
ZMUC	Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark
ZMUO	Zoological Museum, University of Oulu, Finland
ZSM	Zoologische Staatssammlung, Munich, Germany

DNA sequencing

A single leg was removed from each specimen and placed in a 96-well lysis plate that was submitted for analysis at the CCDB (Canadian Center for DNA Barcoding, University of Guelph, Canada) where DNA extraction, PCR amplification, and sequencing were performed following standard high-throughput protocols (deWaard et al. 2008). In total, 5986 specimens of European Gelechiidae, initially pre-identified from external and partially genitalia morphology by several colleagues and cross-checked by PH and OK in dubious cases, were successfully sequenced. Details of specimens,

including complete voucher data, images, and GenBank accession numbers are available on BOLD (Ratnasingham 2018, Ratnasingham and Hebert 2007) in the public dataset "Lepidoptera (Gelechiidae) of Europe" under the DOI: dx.doi.org/10.5883/DS-GELECHEU.

Data analysis

Levels of intra- and interspecific variation in the DNA barcode fragment were calculated under the Kimura 2-parameter (K2P) model of nucleotide substitution using analytical tools in BOLD systems v4.0 (http://www.boldsystems.org). Fifty-three Neighbor-Joining trees (Maximum Composite Likelihood method, default settings), most including representatives of a single genus, were constructed using MEGA X (Kumar et. al 2018) (Suppl. material 2 and 3). Node confidences were estimated using 500 bootstrap replicates. For genera with few species, several morphologically closely related genera were included in a single tree. For calculating these trees only sequences ≥ 500 bp were used, except for ten species where only shorter sequences were available (Suppl. material 1). In those cases where the specimens of a single species were assigned to two or more different BINs, they were discriminated by a letter code. Because of the high number of BINs for *Megacraspedus dolosellus* and *M. lanceolellus*, these taxa were figured in two separate NJ trees with BINs separated as single clusters. Species sharing a BIN, but still with a diagnostic barcode were grouped in separate clusters. A three-letter code (ISO 3166-1 alpha-3, https://en.wikipedia.org/wiki/ISO_3166-1_alpha-3) was used to abbreviate country names.

Identification success was assessed by the Barcode Index Number (BIN) system as implemented on BOLD (Ratnasingham and Hebert 2013). This system employs a two-stage algorithm that groups all sequences > 500 bp that meet defined quality criteria into Operational Taxonomic Units (OTUs) and automatically assigns new sequences, irrespective of their previous taxonomy and origin. Concordance or discordance between BINs and morphological species identification was assessed.

Results

Overview

DNA barcode sequences were recovered from 5986 specimens representing 751 of the 865 species of Gelechiidae described from Europe (Suppl. material 1). In addition, the analysis revealed 65 putative species whose members were each assigned to a different unique BIN. Most sequences (5476) were compliant with the barcode standard as described in BOLD (http://www.boldsystems.org). Most subsequent analyses only considered the 741 species with sequences ≥ 500bp, but ten additional species with sequences ≥ 300 bp were included in the NJ trees. Sequences from 723 species qualified for BIN analysis.

Species delimitation from DNA barcode divergences

Intraspecific DNA barcode variation in the 741 named species with sequences ≥500 bp averaged 0.54%, but this may be an underestimate as sample sizes for 224 taxa were low and only represented by singletons. In respect to the distribution of mean intraspecific DNA barcode variation: 73.1% of sequenced species had variation ranging from 0–1%, 15.8% between 1–2%, 6.3% between 2–3%, and 4.8% > 3%.

Contrastingly, barcode gap analysis resulted in mean distances of 5.58% (maximum 12.75%) to the Nearest Neighbor (NN) with only 5.68% of all species showing a NN distance of 0–1% (Table 2). In this latter group, only four species pairs/triplets (*Dirhinosia cervinella* / *D. interposita*, *Iwaruna biguttella* / *I. klimeschi*, *Teleiodes brevivalva* / *T. italica* / *T. vulgella*, *Xenolechia aethiops* / *X. lindae* / *X. pseudovulgella*) shared barcodes so they could not be discriminated on that basis. In eight other cases, shared DNA barcodes meant that assignments were sometimes unreliable, but these species also possessed unique haplotypes (*Acompsia antirrhinella* / *A. tripunctella*, *Anacampsis blattariella* / *A. populella*, *Bryotropha affinis* / *B. umbrosella*, *Sattleria pyrenaica* / *S. melaleucella*, *Scrobipalpa arenbergeri* / *S. mercantourica*, *Stomopteryx lineolella* / *S. nougatricella*, *Thiotricha subocellea* / *T. coleella*, and partially also *Teleiopsis bagriotella* /*T. diffinis* / *T. paulheberti*). Finally, low distances between *Scrobipalpa alterna* / *S. lutea* and *S. halymella* / *S. stabilis* were only based on a single sequence for each of these species so they may represent additional cases of barcode overlap. On the other hand, five other species pairs with low interspecific divergence could be reliably separated by barcodes (*Monochroa arundinetella* / *M. suffusella*, *Scrobipalpa stangei* / *S. artemisiella*, *Scrobipalpa salinella* / *S. salicorniae*, *Scrobipalpula* spp., *Teleiopsis rosalbella* / *T. albifemorella*). Considering all these cases, DNA barcodes showed either incomplete or no resolution for 31 species (4.2%), while species identification was effective for 710 species (95.8%).

Species delimitation with Barcode Index Number (BIN) system

In total, 5877 sequences were assigned to a BIN. These records were assigned to 992 BINs that belong to 788 putative taxa (Suppl. material 2 and 3). Among these, 723 corresponded with named species, while another 65 belong to a unique BIN that is currently unidentified, but many likely represent additional, unrecognised species. Specimens from another 114 named species were assigned to more than one BIN; members of 68 species were placed in two BINs, while BIN counts for the other 46 species ranged from three to 22 (Table 2).

Altogether 668 (92.4%) of 723 named species have one or more unique BINs, while 55 species (7.6%) share a BIN with up to four species (Table 3). BIN sharing was particularly frequent in six genera (*Acompsia*, *Dirhinosia*, *Iwaruna*, *Scrobipalpula*, *Teleiopsis*, *Xenolechia*) where species often cannot be discriminated by DNA barcodes. However, most specimens in these taxa have diagnostic barcodes and all possess diagnostic morphological characters.

Table 1. 42 Species with Nearest-Neighbour distances of 0–1%.

Species	Mean intra-spec.	Max intra-spec.	Nearest species	Dist. NN
Bryotropha affinis	0.17	0.77	*Bryotropha umbrosella*	0
Bryotropha umbrosella	1.76	3.63	*Bryotropha affinis*	0
Iwaruna biguttella	0.78	2.02	*Iwaruna klimeschi*	0
Iwaruna klimeschi	0	0	*Iwaruna biguttella*	0
Teleiodes brevivalva	0.46	0.46	*Teleiodes vulgella*	0
Teleiodes italica	0.32	0.62	*Teleiodes vulgella*	0
Teleiodes vulgella	0.17	0.5	*Teleiodes italica*	0
Xenolechia aethiops	0.08	0.16	*Xenolechia lindae*	0
Xenolechia lindae	0	0	*Xenolechia aethiops*	0
Xenolechia pseudovulgella	N/A	0	*Xenolechia aethiops*	0
Scrobipalpa alterna	N/A	0	*Scrobipalpa lutea*	0.35
Scrobipalpa lutea	N/A	0	*Scrobipalpa alterna*	0.35
Acompsia antirrhinella	1.39	1.39	*Acompsia tripunctella*	0.46
Acompsia tripunctella	2.59	6.4	*Acompsia antirrhinella*	0.46
Dirhinosia cervinella	0.14	0.32	*Dirhinosia interposita*	0.46
Dirhinosia interposita	0	0	*Dirhinosia cervinella*	0.46
Monochroa arundinetella	0.05	0.15	*Monochroa suffusella*	0.47
Monochroa suffusella	0.52	1.07	*Monochroa arundinetella*	0.47
Scrobipalpula psilella	0.21	0.64	*Scrobipalpula seniorum*	0.53
Scrobipalpula seniorum	N/A	0	*Scrobipalpula psilella*	0.53
Anacampsis blattariella	0.48	2.99	*Anacampsis populella*	0.56
Anacampsis populella	0.22	1.41	*Anacampsis blattariella*	0.56
Teleiopsis albifemorella	0.62	1.42	*Teleiopsis rosalbella*	0.61
Teleiopsis bagriotella	0.91	2.66	*Teleiopsis diffinis*	0.61
Teleiopsis diffinis	1.43	3.26	*Teleiopsis bagriotella*	0.61
Teleiopsis rosalbella	0.22	0.46	*Teleiopsis albifemorella*	0.61
Thiotricha coleella	N/A	0	*Thiotricha subocellea*	0.67
Thiotricha subocellea	0.74	1.4	*Thiotricha coleella*	0.67
Stomopteryx lineolella	N/A	0	*Stomopteryx nugatricella*	0.77
Stomopteryx nugatricella	0	0	*Stomopteryx lineolella*	0.77
Scrobipalpula diffluella	0.54	1.2	*Scrobipalpula tussilaginis*	0.8
Scrobipalpula tussilaginis	0.17	0.46	*Scrobipalpula diffluella*	0.8
Scrobipalpa arenbergeri	0.49	0.77	*Scrobipalpa mercantourica*	0.92
Scrobipalpa artemisiella	0.6	2.5	*Scrobipalpa stangei*	0.92
Scrobipalpa mercantourica	N/A	0	*Scrobipalpa arenbergeri*	0.92
Scrobipalpa salicorniae	0.16	0.46	*Scrobipalpa salinella*	0.92
Scrobipalpa salinella	0.28	0.92	*Scrobipalpa salicorniae*	0.92
Scrobipalpa stangei	0.15	0.31	*Scrobipalpa artemisiella*	0.92
Sattleria melaleucella	1.11	1.87	*Sattleria pyrenaica*	0.93
Sattleria pyrenaica	2.6	3.65	*Sattleria melaleucella*	0.93
Scrobipalpa halymella	N/A	0	*Scrobipalpa stabilis*	0.93
Scrobipalpa stabilis	N/A	0	*Scrobipalpa halymella*	0.93

Potential cryptic diversity – unrevised taxa

High levels of 'intraspecific' barcode variation often reflect overlooked species, but there is no fixed level of divergence that indicates species status. Furthermore, deep barcode splits can also arise as a result of the inadvertent recovery of pseudogenes, as a consequence of hybridisation, or *Wolbachia* infection (Mally et al. 2018, Werren et al. 2008). In Lepidoptera, 2–3% divergence is occasionally viewed as signalling the need for further integrative analysis (Hausmann et al. 2013), but there is clear evidence that

Table 2. 46 species of European Gelechiidae assigned to multiple (3-22) BINs

Species	no. of BINs	Species	no. of BINs
Aproaerema anthyllidella	3	*Teleiopsis paulheberti*	3
Aproaerema karvoneni	3	*Aroga flavicomella*	4
Aroga velocella	3	*Caryocolum amaurella*	4
Brachmia dimidiella	3	*Caryocolum fibigerium*	4
Bryotropha desertella	3	*Caryocolum peregrinella*	4
Bryotropha umbrosella	3	*Caryocolum vicinella*	4
Caryocolum alsinella	3	*Ephysteris promptella*	4
Caryocolum marmorea	3	*Gelechia sabinella*	4
Caryocolum tischeriella	3	*Isophrictis anthemidella*	4
Chionodes fumatella	3	*Megacraspedus imparellus*	4
Chionodes viduella	3	*Metzneria metzneriella*	4
Hypatima rhomboidella	3	*Mirificarma cytisella*	4
Isophrictis meridionella	3	*Athrips amoenella*	5
Megacraspedus binotella	3	*Isophrictis kefersteiniellus*	5
Metzneria aprilella	3	*Megacraspedus brachypteris*	5
Metzneria artificella	3	*Monochroa nomadella*	5
Neofaculta ericetella	3	*Sattleria pyrenaica*	5
Oxypteryx baldizzonei	3	*Acompsia tripunctella*	6
Parachronistis albiceps	3	*Caryocolum schleichi*	6
Ptocheuusa paupella	3	*Oxypteryx libertinella*	7
Stomopteryx flavipalpella	3	*Stomopteryx remissella*	8
Teleiodes flavimaculella	3	*Megacraspedus lanceolellus*	20
Teleiodes luculella	3	*Megacraspedus dolosellus*	22

Table 3. Species of European Gelechiidae which share a BIN.

Species	BIN
Acompsia antirrhinella / A. pyrenaella / A. tripunctella	BOLD:AAJ5937
Anacampsis blattariella / A. populella	BOLD:AAD3256
Aproaerema albipalpella / A. cincticulella	BOLD:ACB8811
Aristotelia brizella / A. confusella	BOLD:AAJ1682
Athrips pruinosella / A. spiraeae	BOLD:AAD2577
Caryocolum arenbergeri / C. blandulella	BOLD:AAV7765
Dirhinosia cervinella / D. interposita	BOLD:ACB0757
Iwaruna biguttella / I. klimeschi / I. robineaui	BOLD:AAU3602
Metzneria fulva / M. torosulella	BOLD:ADM4637
Monochroa arundinetella / M. suffusella	BOLD:AAF9390
Monochroa palustrellus / M. saltenella	BOLD:AAF2711
Sattleria melaleucella / S. pyrenaica	BOLD:AAC5037
Scrobipalpa alterna / S. lutea	BOLD:ADR5476
Scrobipalpa amseli / S. hyssopi	BOLD:ADL8424
Scrobipalpa artemisiella / S. stangei	BOLD:AAE9838
Scrobipalpa halymella / S. stabilis	BOLD:AAV9005
Scrobipalpa salicorniae / S. salinella	BOLD:AAF1193
Scrobipalpula diffluella / S. psilella / S. ramosella / S. seniorum / S. tussilaginis	BOLD:AAF1106
Stomopteryx lineolella / S. mongolica / S. nugatricella	BOLD:ACB3380
Teleiodes brevivalva / T. italica / T. vulgella	BOLD:AAE9855
Teleiopsis albifemorella / T. rosalbella	BOLD:AAB6930
Teleiopsis bagriotella / T. diffinis / T. paulheberti	BOLD:ACE4927
Teleiopsis bagriotella / T. diffinis	BOLD:ACE6105
Xenolechia aethiops / X. lindae / X. pseudovulgella	BOLD:AAE1445

no such threshold values exist (see e.g., Kekkonen et al. 2015). In the present dataset 146 of 741 nominal species possessed a maximum intraspecific divergence of > 2%, 88 species > 3%, while 33 species showed greater than > 5% (Table 4).

In some recently revised taxa with high, geographically structured intraspecific barcode divergence such as *Megacraspedus* (Huemer and Karsholt 2018) or the *Oxypteryx libertinella* species-group (Huemer et al. 2013), no evidence for cryptic diversity was found. However, even lower 'intraspecific' barcode divergence may reflect cases of either allopatric or sympatric speciation, as proven e.g., for the genus *Sattleria* (Huemer and Hebert 2011, Huemer and Timossi 2014). In consequence, several species with unusual genetic pattern need to be carefully re-assessed as they may include additional species. Cryptic diversity was, for example, already suspected for some *Caryocolum* (Huemer et al. 2015) or *Stomopteryx remissella*, but may also be detected in recently revised genera such as *Acompsia* or *Chionodes* (Huemer and Karsholt 2002, Huemer and Sattler 1995).

A further group of unrevised species in our dataset includes 65 unidentified DNA barcode clusters which were assigned to separate BINs (Table 5). Many of these cases are likely to represent undescribed species or alternatively, they may represent described species that currently lack barcode coverage. Altogether 26 genera representing approximately one-quarter of European genera are candidates for additional taxa. In fact, four genera (*Aproaerema*, *Aristotelia*, *Monochroa*, *Scrobipalpa*) are each represented by more than five unidentified clusters. For detailed comments on these cases, see Huemer and Karsholt (2020).

Table 4. 33 species of European Gelechiidae with a maximum intraspecific barcode divergence > 5%.

Species	Mean intra-spec.	Max intra-spec.
Megacraspedus dolosellus	7.49	13.76
Megacraspedus lanceolellus	7.37	12.51
Monochroa sepicolella	5.15	9.78
Megacraspedus brachypteris	4.36	7.82
Stomopteryx remissella	2.69	7.47
Ephysteris diminutella	3.87	7.15
Sophronia sicariellus	1.34	7.06
Caryocolum cauligenella	1.86	7.00
Acompsia pyrenaella	3.58	6.92
Caryocolum saginella	2.17	6.86
Dichomeris rasilella	3.31	6.67
Monochroa nomadella	3.72	6.58
Caryocolum schleichi	3.93	6.47
Acompsia tripunctella	2.59	6.40
Megacraspedus teriolensis	3.07	6.38
Caryocolum fibigerium	3.41	6.31
Chionodes fumatella	2.6	6.30
Oxypteryx baldizzonei	3.9	6.29
Oxypteryx wilkella	1.5	6.29
Dichomeris juniperella	2.82	6.24

Species	Mean intra-spec.	Max intra-spec.
Parapodia sinaica	2.97	5.95
Megacraspedus balneariellus	3.97	5.95
Mirificarma burdonella	5.9	5.9
Caryocolum peregrinella	3.56	5.71
Caryocolum alsinella	2.11	5.60
Oxypteryx libertinella	2.65	5.48
Aproaerema suecicella	2.43	5.44
Megacraspedus imparellus	4.05	5.43
Isophrictis anthemidella	2.92	5.3
Catatinagma trivittellum	5.24	5.24
Pexicopia malvella	1.1	5.23
Acompsia maculosella	2.16	5.19
Ephysteris promptella	3.31	5.12

Table 5. Unidentified species of European Gelechiidae with unique BINs.

Taxon	BIN	Taxon	BIN
Anarsia	BOLD:ADE9567	*Ivanauskiella*	BOLD:ACB0708
Anarsia	BOLD:ADE9710	*Megacraspedus*	BOLD:ACZ8654
Apatetris	BOLD:AAV7596	*Megacraspedus*	BOLD:ADY4582
Apatetris	BOLD:ABA4360	*Mesophleps*	BOLD:AAU3614
Aproaerema	BOLD:AAT9258	*Mesophleps*	BOLD:ADM4492
Aproaerema	BOLD:ACF7323	*Metzneria*	BOLD:ABW1820
Aproaerema	BOLD:ADG7311	*Metzneria*	BOLD:ACB3385
Aproaerema	BOLD:ADL8444	*Metzneria*	BOLD:ADM8252
Aproaerema	BOLD:ADL9068	*Monochroa*	BOLD:ACF6594
Aproaerema	BOLD:ADL9069	*Monochroa*	BOLD:ACS5726
Aristotelia	BOLD:AAU2122	*Monochroa*	BOLD:ACW2532
Aristotelia	BOLD:AAV7599	*Monochroa*	BOLD:ADL7906
Aristotelia	BOLD:ABV2430	*Monochroa*	BOLD:ADL9322
Aristotelia	BOLD:ACC2990	*Monochroa*	BOLD:ADR3927
Aristotelia	BOLD:ACK0360	*Neofriseria*	BOLD:ADR5460
Aristotelia	BOLD:ADC8189	*Ochrodia*	BOLD:ACE0260
Aristotelia	BOLD:ADK9648	*Oxypteryx*	BOLD:ACR9491
Aristotelia	BOLD:ADL8520	*Oxypteryx*	BOLD:ACS7858
Aristotelia	BOLD:ADL8769	*Oxypteryx*	BOLD:ACS7859
Aristotelia	BOLD:ADL9120	*Psamathocrita*	BOLD:ADF0071
Aristotelia	BOLD:ADM4599	*Psamathocrita*	BOLD:ADL7901
Aristotelia	BOLD:ADY0927	*Ptocheuusa*	BOLD:AAV7056
Brachmia	BOLD:ADM5065	*Scrobipalpa*	BOLD:AAV4547
Caulastrocecis	BOLD:ADM1812	*Scrobipalpa*	BOLD:ACT3383
Caulastrocecis	BOLD:ADR7056	*Scrobipalpa*	BOLD:ACT4605
Chrysoesthia	BOLD:ADM8914	*Scrobipalpa*	BOLD:ADF0070
Chrysoesthia	BOLD:ADN7772	*Scrobipalpa*	BOLD:ADG5400
Dichomeris	BOLD:ADI2574	*Scrobipalpa*	BOLD:ADL6932
Epidola	BOLD:ADF2272	*Scrobipalpa*	BOLD:ADL7117
Gelechia	BOLD:ADF0061	*Sophronia*	BOLD:ADF5021
Gelechiidae	BOLD:ADO2643	*Stomopteryx*	BOLD:ADM5270
Isophrictis	BOLD:ADF3165	*Telphusa*	BOLD:ADM5148
Isophrictis	BOLD:ADI3246		

Discussion

During the past decade, several national DNA barcoding campaigns have led to the development of an increasingly well-parameterised DNA barcode library for European Lepidoptera. However, these projects have mainly focused on the fauna of central and northern Europe. As a consequence, genetic coverage for species in the Mediterranean region remains patchy. Reflecting this fact, continent-wide analysis has only considered a few groups so far, such as Nepticulidae (van Nieukerken pers. comm.), Gracillariidae (Lopez-Vaamonde pers. comm.), Elachistinae (Mutanen et al. 2011), Depressariidae (Buchner pers. comm), Geometridae (Hausmann et al. 2013, Müller et al. 2019), and Papilionoidea (Dincă pers. comm.). By contrast, for most families either few DNA barcodes exist, or comprehensive genetic analysis is not available.

The current DNA barcode library makes it clear that the Gelechiidae is a particularly good example of the serious gaps in the knowledge of European biodiversity. Nearly a quarter of current fauna has been described since 1990 (Fig. 3). This gap between European gelechiid diversity and adequate coverage in published alpha-taxonomy is most probably a result of: 1) the small number of gelechiid experts, 2) the lack of adequate vouchers for phenotypic and molecular study 3) the frequently cryptic morphology making them less attractive to non-expert workers, and 4) the infrequent consideration of molecular data to assess taxonomic boundaries.
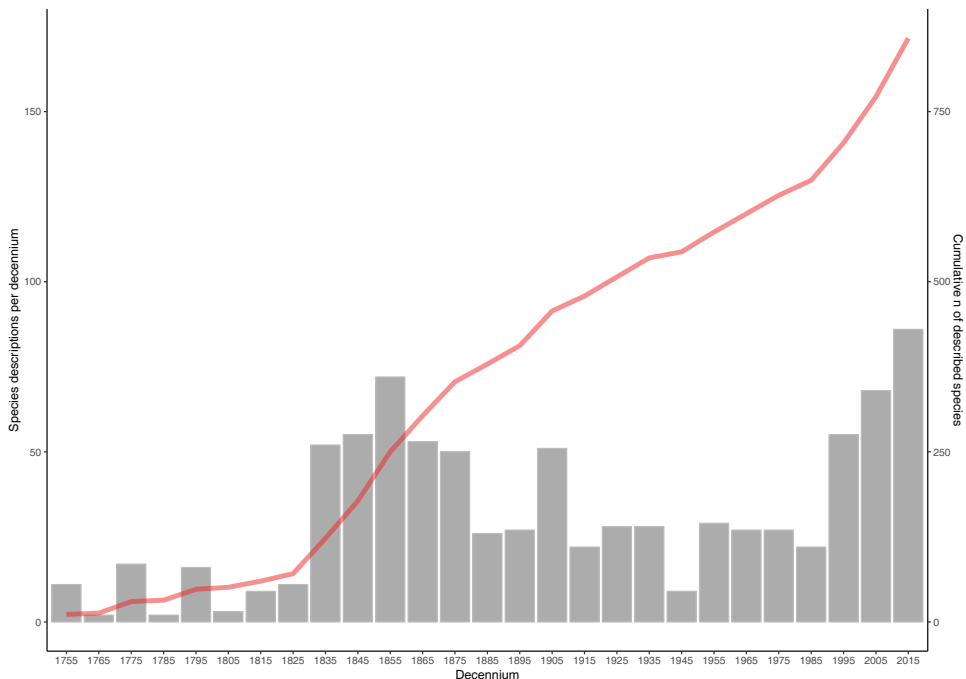
Figure 3. Periods of descriptions of European Gelechiidae.

In the present study, DNA sequences revealed a high level of possible cryptic diversity in European Gelechiidae, despite extensive revisionary work over the last decades (see e.g., Huemer and Karsholt 1999, 2010). Although almost 96% of all 741 species possessed unique barcodes, intraspecific divergences exceeded 2% in nearly a fifth of currently recognised species, and 33 of these cases of divergence values exceeded 5%, values that likely signal overlooked species.

The intraspecific DNA barcode variation is reflected in some taxa as allopatric divergence, but in other cases, it reflects sympatric deep splits. However, few of these species have received detailed taxonomic assessment such as the recent comprehensive study on *Megacraspedus* (Huemer and Karsholt 2018). In many other unrevised genera/species-groups a significant increase in species diversity is likely. The major gaps in taxonomic treatment of European Gelechiidae are further demonstrated by the large number of unidentified genetic clusters revealed by the present investigation as many of these 65 putative taxa are likely to represent undescribed species.

Conclusions

By providing coverage for 751 species of European Gelechiidae, the current DNA barcode library represents the largest release in terms of species diversity for any family of Lepidoptera on this continent. The results reveal unexpected genetic diversity in many taxa as well as numerous unidentified taxa. This indicates that the alpha-taxonomy of this family, still requires serious attention despite one-quarter of the known species described after 1990. The current results indicate that the Gelechiidae remain one of the most taxonomically challenging families of Lepidoptera in the World as complete coverage of even European fauna will require extensive effort. However, the DNA barcode library generated in this study will allow these revisionary studies to target groups that are particularly problematic, accelerating the documentation of the fauna.

Acknowledgements

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Supplementary material 1

Barcoded species

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Data type: species data

Link: https://doi.org/10.3897/zookeys.921.49199.suppl1

Supplementary material 2

NJ trees 1–53

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Supplementary material 3

Specimen data to NJ trees 1–53

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