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**Studies on the *Diapriidae* (Hymenoptera, Proctotrupoidea).  
Part I. Taxonomic remarks on the subfamily *Belytinae*  
with particular reference to the tribus *Pantolytini***

**Abstract.** This is the first of a series of papers revising the genera of *Diapriidae* with emphasis on the Central European fauna. The aim of this work should be to improve our knowledge of this poorly studied group of *Proctotrupoidea* as well as to provide useful keys, and to work out a new classification based on the interpretation of apomorphies inferred. The genera are to be treated with respect to their presumed relationships. This paper deals with the subfamily *Belytinae* with particular reference to the tribus *Pantolytini*. The taxonomic value of adult characters and their taxonomic implications are discussed. Identification keys for all genera of *Pantolytini* are provided. A new classification for *Pantolytini* is proposed.

INTRODUCTION

*Diapriidae* is a large family of *Proctotrupoidea* of worldwide distribution and with large species diversity. Since the edition of KIEFFER's monograph (1916) on world species, little attention has been paid to this group of *Proctotrupoidea* as compared to related families of *Hymenoptera*. Those who have tried to use KIEFFER's keys for identification of species found that they are unsatisfactory. KIEFFER's diagnostic characters proved to be varying in most cases, obscuring the delimitation of species based on them. In spite of the comprehensiveness of that work, many students dealing with taxonomy of *Diapriidae* found it inapplicable in many respects. The characters used by KIEFFER are mostly inconsistent with true relationships of taxa considered. Most of the genera KIEFFER created turned out to be artificial assemblages of species included because of their external similarities. Neglect of intraspecific variability

resulted in many invalid nominal species, and the other to be erroneously interpreted. Revisionary studies of recent authors revealed these shortcomings and pointed out the necessity of a complete revisionary study. Unfortunately, it seems to be highly improbable to finish this work within a short period because many crucial types are difficult to obtain. The Diapriid types seem to have had an unfortunate history because KIEFFER neither designated his type specimens nor indicated their depository properly. It is thought that most of his types are deposited in National Museum in Paris. Recent authors made attempts to improve upon KIEFFER's work with varying success. NIXON (1957) revised some types, particularly those in British Museum. He provided excellent keys to the British species widely applicable to the European fauna. Unfortunately, his work bears some shortcomings due to the limited numbers of types he studied. Some crucial species were not properly studied and were interpreted in a subjective way. Consequently those species have been interpreted erroneously and new invalid taxa were established. MASNER (1958, 1964) pointed out that the delimitation of many genera in the past was so obscured and their description so vague that they resulted in different interpretations. For example, most of genera established by FOERSTER (1856) have no species included. ASHMEAD (1893) interpreted FOERSTER's genera subjectively basing on original description and assigned the first species to them. KIEFFER (1910 [1907-1911]) revised FOERSTER's collection. He identified and redescribed FOERSTER's genera, designated some type species coming from that collection and included his new species into these newly defined genera. Since that time taxonomic problems have been arisen resulting in students following either ASHMEAD or KIEFFER. These problems were solved by the fixation of the type-species as the first species included in genus (Bull. zool. Nomencl., 4: 160, 346-1950). Nevertheless, all the genera described so far need to be revised and clearly defined. The framework for this work will provide a list of type-species designated by MUESBECK and WALKLEY (1956). Since several authors have dealt with *Belytinae*. WALL (1967) analyzed taxonomically significant characters used for classification, provided keys. HELLÉN (1963) treated the fauna of Finland and adjacent areas providing diagnoses and useful keys. KOZLOV (1978) keyed the genera and species from the European U.S.S.R. His keys are broadly applicable to European *Diapriidae* fauna. MASNER (1977) monographed the genus *Ismarus* of the Nearctic region. There are also minor recent contributions dealing with particular problems in *Belytinae* having no adverse impact on *Belytinae* taxonomy.

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## Adult characters selected from the standpoint of taxonomic significance

The whole tribe *Pantolytini* is characterized by a uniformity of ovipositor retaining many primitive characters. The apomorphy is its insertion versus exertion expressed in many primitive families of *Hymenoptera*. In the *Belytinae* the inserted condition is the ancestral one. In derived groups the long ovipositor tends to become shortened, resulting in a thin delicate structure. In the specialized state the ovipositor does not exceed the length of the last tergite and the third valvulae enlarge to form flat, black sheaths. This ovipositor is adapted for direct oviposition into host. A return to parasitism of cryptic hosts necessitated adaptations of the inserted telescoping ovipositor. Telescoping has arisen from semicircular, modified terminal metasomal segments of the tergites and sternites, closely fitted. In the extreme condition, the length of the telescopic part of metasoma exceeds the gastral trunk thus forming a distinctly separated part of metasoma (= postabdomen of some authors). The inserted long ovipositor of the *Pantolytini* sometimes also occurs in the genus *Pantoclis* FOERSTER. However this ancestral character is supplemented by a number of apomorphies unique to *Pantoclis* only. Therefore *Pantoclis* must be excluded from *Pantolytini*. Common ancestry of all the species now assigned to *Pantolytini* depends on many different apomorphies not the primitive state of the ovipositor alone. The radiation of unique characters may thus obscure the true relationships among the genera. Since the ovipositor of *Belytinae* is highly modified due to the rate of adaptiveness to the modus of oviposition it is not useful for discriminating among higher taxa. Similar improvements of ovipositor were independently achieved in unrelated lineages such as *Cinetini* (*Cinetus* JURINE, *Aclista* auct., *Eumiota* HELLEN) and *Belytini* (*Leptonetus* MASNER, *Diphora* FOERSTER). In the *Belytini* both types of ovipositors occur: the ancestral state (e.g. *Pantoclis* with intergrading state) and the derived state (e.g. *Belyta* JURINE). The long inserted ovipositor of *Pantolytini* caused some modifications of the structure of metasoma. This has been achieved in both lineages of *Pantolytini* (subtribes *Pantolytina* and *Psilommina* nov.) in different way. In *Pantolytina* the terminal gastral (= metasomal) segments, especially the 8th and 9th are enormously extended longitudinally resulting in a sharply pointed metasoma several times longer than the mesosoma. In *Psilommina* the proximal sternal part tends to be projected anteriorly into a pocket-like prominence where basal parts of ovipositor are deposited.

Various metasomal modifications of females are reflected in different structural arrangements of the male genitalia. They provide more useful evidence for relationships of species because they tend to be modified at a lesser rate than the ovipositor. Males have tendency to evolve fewer specializations because of a more uniform modus vivendi. The macroscopic uniformity of many species in many related genera makes their determination difficult, but provides

good evidence of their mutual relationships. In *Pantolytina* and *Psilommina* male genitalia are arranged into two different looking assemblages. In *Pantolytina* they are large, with dentes situated horizontally on the phallus and lamina volsellaris attached to, but rarely fused with, dentes. In *Psilommina* only the genus *Psilomma* exhibits a similar arrangement, but paramerae become more tapered apically. Other genera having genitalia considerably prolonged and narrowed, dentes rotated into a vertical position and became completely fused with lamina volsellaris. In the plesiomorphic state the lamina volsellaris is tightly attached to dentes, but never fused with them. The tendency of the dentes to rotate and fuse with the lamina volsellaris is characteristic for the *Psilommina*. However in *Pantoclis* (see above), in which a long ovipositor is also preserved, the arrangement of the genitalia is quite different. Dentes are reduced and rotate vertically, but remain completely free from the lamina volsellaris. The latter are joined to the wall of phallus by means of a soft membrane which allows considerable movability.

Wing venation is uniform in *Psilommina* and provides a good diagnostic character for the genera included. In comparison with *Pantolytina*, a poorly developed network in *Psilommina* is a derived condition. The radial cell is open, both radialis and postmarginalis are absent and sometimes the radialis is faintly indicated as a spurious line paralleling the fore-wing margin. The stigmalis is perpendicular to the marginalis, but in *Synaera* tends to be reduced to a thin, tubercular projection of the marginalis. The length of marginalis becomes larger than the abscissa between marginalis and basalis. A well developed network of veins is a plesiomorphic state within *Belytinae*. Therefore, the closed radial cell occurring in *Acropiasta* is a primitive condition, and open radial cell, with a gradually regressing radialis is a derived one. The regression of radialis may be described as either cell diminishment (*Meuselia*, *Opazon*) or a complete reduction of radial cell by obliteration of radialis (*Pantolyta*). Hind wings (in macropterous specimens) are large in *Psilommina* and stenopterous in *Pantolytina*. The tendency toward wing reduction is expressed in both lineages in the same way. Particular pterygopolymorphic specimens appear very different from the macropterous ones, and were treated as separate species by earlier authors. The frequency of particular morphs is influenced by local environmental factors. The major one seems to be food supply. That could explain the periodicity of occurrence of particular morphs in populations. For example there are mostly micropterous morphs in *Synaera brachialis* NEES, total absence of macropterous morphs in *Anommatium* and scarcity of micropterous females in *Acropiasta*, *Meuselia* and *Pantolyta*. The discovery of scarce as well as unknown morphs seems to be a matter of collecting methods rather than their absence.

The cylindrical shape of petiolus is a plesiomorphic state. The derived state is the shortening of the petiolus and its widening medially, becoming heart-shaped. In *Acanosema* the shape of petiolus is not stabilized because of high

pterygopolymorphism. The macropterous morphs tend to have petiolus more cylindrical as compared to micropterous ones. Functional interpretation of this structure, despite of its uniqueness in *Diapriidae*, is a matter of conjecture. The analysis of a great number of specimens of *Acanosema* species showed the presence of a modified petiolus connected with the presence of a sternal projection (petiolus of specimens with an extremely prominent sternal segment is heart-shaped, and vice versa). In *Pantolytina*, the petiolus remains simple and unmodified although considerably shortened.

The pronotum bears some unique structures peculiar to *Psilommina*. Medial pronotal pits become fused in the derived condition resulting in a medial pronotal bridge. Lateral pronotal pits are faintly indicated in *Psilomma* (plesiomorphic state), and fully developed in *Acanosema*, where they are covered with dense white pubescence. The evolution of pubescent fovea is accompanied by thickening of pubescence along the foramen occipitale, collare, petiolus and proximal part of the gaster (*Acanosema*, *Synacra*). The presence of dense pubescence is assumed to be a specialized state with special adaptative value connected with myrmecophily (*Synacra* and *Acanosema rufum* KIEFFER are associated with ants). The proximal part of the pronotum is raised and distinctly separated from the lower cervical part thereby covering lateral pits. Pronotal shoulders are prominent. In the derived state, the separation fades out and the pronotal shoulders become rounded, and the lateral pits become visible. In *Pantolytina*, medial pits are constantly shallow, lateral pits are lacking.

As to antennae, the subsequent reduction of female flagellomera is a characteristic trait in *Psilommina*. Former authors applied a different number of flagellomeras to discriminate higher taxa in *Diapriidae*. But recent comparative morphological studies reveal this character has little taxonomic value because flagellomeras can be reduced in unrelated taxa as well as within one species (*Anommatium ashmeadi* MAYR). In *Psilommina*, the number of antennal segments intergrade from the ancestral state (15 segments) to the most derived one (12 segments). The reduction of antennal segments is accompanied by a great number of other apomorphies as follows: beak-like mandibles, raised flange of scapus margin with ear-like tiny projections, reduction of wing venation, transformation of petiolus and thickening of pubescence. The 15-segmented antennae include all species of *Psilomma*, *Acanosema* and *Cardiopsilus*; 14-segmented *Acanopsilus* and *Polypeza*; 13-segmented, a new undescribed species related to *Cardiopsilus*; 12-segmented, *Sundholmiella*, *Synacra* and a new undescribed species related to *Acanopsilus*. These groupings seem to show a successive decrease in the number of flagellar segments. In *Pantolytina* the number of segments remains constant, excluding the aberrant species *Anommatium ashmeadi* occupying an isolated position within *Pantolytini*. This tendency towards the decrease in number of antennal segments is seen in *Cinetini*, where species with 15, 14 and 13-segmented antennae have been ascertained. The distal margin of scape is either simple (plesiomorphous state), or raised

into a flange armed with two tiny teeth (apomorphous state). Genera with this derived condition belong to the more specialized taxa in *Pantolytini* (*Synacra*, *Polypeza*, *Acanosema* in *Psilommina*; *Opazon* in *Pantolytina*).

Mandibles briefly overlap apically in the primitive state. The inner mandibular tooth may be short (plesiomorphous) or extended and reaching the length of the outer tooth (apomorphous). Both in *Synacra* and *Opazon* the mandibular base becomes folded-up due to shortening of the distance between the sockets. Consequently, mandibles are extended longitudinally with the outer tooth turned down, appearing beak-like. Since this modification occurs in other unrelated taxa of *Diapriidae*, its taxonomical significance is of limited value. In *Pantolytini* this condition diagnoses the genera *Synacra*, *Sundholmiella*, *Polypeza* in *Psilommina* and the genus *Opazon* in *Pantolytina*.

Parapsidal sutures are either present or absent in *Pantolytini*. The absence of parapsidal sutures is confined to the most derived genera (*Anommatium*, *Synacra*, *Sundholmiella*).

#### Reclassification of the tribus *Pantolytini*

Based on the results of character analysis discussed above, a new classification of the tribus *Pantolytini* is proposed. Tribus *Pantolytini* is characterized by primitive state of ovipositor corresponding to the general scheme of Terebrant *Hymenoptera* except it is inserted. Both arrangements of the male genitalia as well as the reduction of the radial vein divide *Pantolytini* in two closely related lineages: *Psilommina* and *Pantolytina* erected as new subtribes. The beak-like mandibles evolved independently in both complexes. They distinguish the genera *Synacra* and *Sundholmiella* from the remainder of *Psilommina*, and genus *Opazon* from others *Pantolytina*. Particular genera are delimited as indicated in the key to genera. The tribal name *Pantolytini* was at first proposed by HELLEN (1964). The improved classification of *Pantolytini* is proposed as follows:

Tribus: *Pantolytini*

A. Subtribus: *Pantolytina* stat. nov.

Genera:

*Acropiesta* FOERSTER, 1856, Hymenopterologische Studien, 2: 129, 135 (no species); type species: *Acropiesta flavicauda* ASHMEAD, 1893, designated by MUESEBECK and WALKLEY, 1951, in MUESEBECK et al., U.S. Dept. Agr., Agr. Monogr., 2: 689.

*Pantolyta* FOERSTER, 1856, Hymenopterologische Studien, 2: 128, 130, 135, 136 (no species); type species: *Pantolyta atrata* FOERSTER, 1861 (first included species).

*Meuselina* KIEFFER, 1909, Ann. Soc. Sci. Bruxelles, **33**: 391; type species: *Meuselina fuscicornis* KIEFFER, 1909 (by original designation).

*Opazon* HALIDAY, 1857, Nat. Hist. Rev., **4**: 170; type species: *Belyta (Opazon) parvula* HALIDAY, 1857 (by monotypy).

*Anommatium* FOERSTER, 1856, Hymenopterologische Studien, **2**: 130, 131, 140 (no species); type species: *Anommatium ashmeadi* MAYR, 1904 (first included species).

B. Subtribus: *Psilommina* nov.

Genera:

*Psilomma* FOERSTER, 1856, Hymenopterologische Studien, **2**: 128, 130, 132 (no species); type species: *Psilomma fusciscapis* FOERSTER, 1861 (first included species).

*Cardiopsilus* KIEFFER, 1908 [1907–1911], in ANDRÉ: Spec. Hym. Eur. Alg., **10**: 360, 405; type species: *Cardiopsilus productus* KIEFFER, 1908 [1907–1911] (by monotypy).

*Acanosema* KIEFFER, 1908 [1907–1911], in ANDRÉ: Spec. Hym. Eur. Alg., **10**: 360, 367, 407 (four species); type species: *Acanosema rufum* KIEFFER, 1908 [1907–1911] (by original designation).

*Synaera* FOERSTER, 1856, Hymenopterologische Studien, **2**: 128, 130, 134 (no species); type species: *Diapria brachialis* NEES, 1834, designated by ASHMEAD, 1893, U.S. Nat. Mus. Bull., **45**: 400.

*Sundholmiella* HEDQUIST, 1975, Ent. Tidskr., **96**: 52–53; type species: *Prosynaera giraudi* KIEFFER, 1910 [1907–1911] (by original designation).

*Polypeza* FOERSTER, 1856, Hymenopterologische Studien, **2**: 123, 127 (no species); type species: *Polypeza pergandei* ASHMEAD, 1893 (first included species).

**Key to the genera of *Pantolytini***

1. Outer pronotal pits present, densely pubescent; if pubescence not developed, then marginalis always longer than vein abscissa between basalis and marginalis; radial cell open or completely absent (*Psilommina*) . . . 2.
- Outer pronotal pits always absent, radial cell closed; if open, the marginalis always shorter than abscissa between basalis and marginalis (*Pantolytina*). . . . . 7.
2. Mandibles simple, overlapping apically. . . . . 3.
- Mandibles beak-like, joining mesally. . . . . 5.
3. Radial cell always missing; inner mandibular tooth as long as outer one; alate species only. . . . . *Psilomma*.
- Radial cell indicated as a spurious line parallel to the front wing margin; inner mandibular tooth shorter than the outer one; pterygopolymorphism frequent. . . . . 4.
4. Scapal flange absent; eyes hairy. . . . . *Cardiopsilus*.

- Scapal flange developed; eyes smooth. . . . . *Acanosema*.
- 5. Body compressed; antennal sockets armed with sharp tooth anteriorly. . . . . *Sundholmiella*.
- Body oval; antennal sockets smooth. . . . . 6.
- 6. Petiolus cylindrical with long and thin pubescence; female antennae 14-segmented; the first gastral sternite simple anteriorly, without thick pubescence. . . . . *Polypeza*.
- Petiolus rounded with convex medial surface bearing short dense white pubescence; female antennae 12-segmented; base of the first gastral sternite hump-like, with dense pubescence. . . . . *Synacra*.
- 7. Mandibles beak-like, attached to each other mesally; radial cell always short, at most as long as marginalis. . . . . *Opazon*.
- Mandibles simple, overlapping apically. . . . . 8.
- 8. Head transverse in frontal view, mandibles not prominent; female pale, wingless, the number of antennal segments reduced to 14–13; palpal segments in female reduced; parapsidal sutures in female absent. . . . . *Anommatium*.
- Head oblong in frontal view with mandibles slightly prominent; female antennae 15-segmented; parapsidal sutures always present. . . . . 9.
- 9. Radial cell open, body length below 2mm. . . . . *Pantolyta*.
- Radial cell closed, body size variable. . . . . 10.
- 10. Radial cell longer than marginalis, if as long as marginalis, the body longer than 2mm. . . . . *Acropiesta*.
- Radial cell shorter than marginalis, if as long as marginalis, the body length not exceeding 2mm. . . . . *Meuselina*.

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## STRESZCZENIE

[Tytuł: Badania nad *Diapriidae* (*Hymenoptera*, *Proctotrupoidea*). Część I. Uwagi taksonomiczne na temat podrodziny *Belytinae* ze szczególnym uwzględnieniem plemienia *Pantolytini*]

Praca ta jest pierwszą z serii rewizji rodzajów *Diapriidae*, zwłaszcza należących do fauny Europy Środkowej. Proponowana tu ponadgatunkowa klasyfikacja plemienia *Pantolytini* jest wynikiem zastosowania metody analizy kładystycznej wybranych cech o największej wartości taksonomicznej, rozpatrywanych pod kątem ich przypuszczalnego apomorfizmu. Przeanalizowano budowę pokładełka, genitaliów samców, skrzydeł, stylika, przedplecza, czułków, żuwaczek oraz obecność lub brak zagłębień parapsydialnych. Stwierdzono, że podstawową wspólną cechą całego plemienia jest prymitywne pokładełko zbliżone do typu wyjściowego, właściwego dla owadziarek (*Terebrantes*). Na podstawie charakteru użyłkowania skrzydeł i struktury genitaliów samców wyróżniono dwie wyraźnie wyodrębnione linie — podplemiona *Pantolytina* (z rodzajami *Pantolyta*, *Acropiesta*, *Meuselia*, *Opazon*, *Anommatium*) i *Psilommina* (z rodzajami *Psilomma*, *Cardiopsilus*, *Acanosema*, *Synaera*, *Sundholmiella*, *Polypeza*). Podano także klucz do oznaczania europejskich rodzajów plemienia *Pantolytini*.

## РЕЗЮМЕ

[Заглавие: Исследования по *Diapriidae* (*Hymenoptera*, *Proctotrupoidea*). Часть I. Замечания по таксономии подсемейства *Belytinae* с особым учетом племени *Pantolytini*]

Настоящая публикация является первой из серии посвященной ревизии родов из семейства *Diapriidae* а особенно представителей фауны Центральной Европы.

Целью этих работ будет углубление наших познаний об этой слабо изученной группе *Proctotrupoidea*, как и составление нужных ключей, а также разработка новой классификации, основанной на интерпретации апоморфических признаков. Роды рассматриваются в связи с их предполагаемыми филогенетическими связями (родством). Настоящая работа посвящена подсемейству *Belytinae*. Дискутируется таксономическая пригодность избранных таксономических признаков имаго и их таксономическое значение. Приведен ключ для определения всех родов, входящих в состав племени *Pantolytini*. Предложена новая классификация племени *Pantolytini*.

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