ABSTRACT

Title of Dissertation: SYSTEMATICS OF DIPARINAE (HYMENOPTERA:
                          PTEROMALIDAE), AND THEIR POSITION WITHIN THE
                          BROADER CONTEXT OF PTEROMALID PHYLOGENY

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Chalcidoidea, one of the largest superfamilies of parasitic Hymenoptera, has major importance in the biological control of insect pests. However, phylogenetic relationships both within and between chalcidoid families have been poorly understood, particularly within Pteromalidae, one of largest families. This study approaches the problem of pteromalid phylogeny from two directions, coupling a detailed morphological revision of one of the most divergent and poorly-known subfamilies of pteromalids (Diparinae) with a broad, exemplar-based molecular study that seeks to place this subfamily in the broader context of pteromalid and chalcidoid phylogeny. First, a morphological phylogenetic analysis of the world genera of Diparinae is provided based on 76 characters. Diparinae is supported as monophyletic based on the presence of a cercal brush in all analyses. The cercal brush, in combination with the absence of a smooth, convex dorsellum, is diagnostic for Diparinae. *Liepara* Boucek (Pteromalidae)

and *Bohpa* Darling (Pteromalidae: Ceinae) both appear as sister-groups to Diparinae in different analyses. The phylogenetic analysis is used to develop a new classification scheme, under which Diparinae consists of 116 species in 14 genera. Three genera and 14 species are described as new, and a key to all genera is provided. Second, forty-two taxa broadly representing Chalcidoidea and more specifically Pteromalidae were sequenced for 4620 bp of four nuclear protein-coding genes, including 1719bp of CAD, 708bp of DDC, 1142bp of enolase, and 1044bp of PEPCK. The combined data set was analyzed using maximum likelihood methods, and the AU test was used to test support for non-monophyly of taxonomic groups which appeared para- or poly-phyletic in the tree. Phylogenetic relationships that have been supported by previous morphological and molecular evidence were recovered (e.g., monophyly of Chalcidoidea), as was the monophyly of groups well supported by morphology but resolved as polyphyletic in previous molecular analyses (e.g., Chalcididae). The monophyly of Pteromalidae and the pteromalid subfamily Colotrechninae are both strongly rejected (p<0.001). New hypotheses are proposed for relationships within Chalcidoidea, including Eutrichosomatinae (Pteromalidae) as the basal lineage of the perilampid/eucharitid clade. This study demostrates that molecular and morphological data can provide reciprocal illumination for understanding relationships within Chalcidoidea.

SYSTEMATICS OF DIPARINAE (HYMENOPTERA: PTEROMALIDAE), AND
THEIR POSITION WITHIN THE BROADER CONTEXT OF PTEROMALID
PHYLOGENY

by

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(Hymenoptera: Pteromalidae)

Abstract

A morphological phylogenetic analysis of the world genera of Diparinae

(Hymenoptera: Pteromalidae) is provided, and the generic classification is revised. A

hypothesized phylogeny is given based on 76 characters, primarily from adult females.

The diparines are supported as monophyletic in all analyses based on 4-6

synapomorphies depending on their sister-group, including the presence of a cercal brush

which is synapomorphic in all analyses. The cercal brush, in combination with the

absence of a smooth, convex dorsellum, is diagnostic for Diparinae. *Liepara* Boucek

(Pteromalidae: subfamily *inquirenda*) and *Bohpa* Darling (Pteromalidae: Ceinae) both

appear as sister-group to Diparinae in different analyses. In the proposed classification

scheme, Diparinae consists of 116 species in 14 genera. Nine genera are removed from

Diparinae, two of which are placed in synonymy: *Calolelaps* Timberlake,

Dinarmolaelaps Masi, *Mesolelaps* Ashmead, *Neolelaps* Ashmead, and *Stictolelaps*

Timberlake are placed in Pteromalinae (Pteromalidae), while *Seyrigina* Risbec is placed

in Eulophinae (Eulophidae); *Diparisca* Hedqvist is synonymized under *Spalangiopelta*

Masi (Pteromalidae: Ceinae); *Bekiliella* Risbec is synonymized under *Notanisus* Walker

(Pteromalidae: Cleonyminae); and *Liepara* Boucek and the tribe Lieparini Boucek are

placed in Pteromalidae without a subfamily association. Eleven new generic synonyms

are proposed: *Alloterra* Kieffer, *Diparomorpha* Hedqvist, *Grahamisia* Delucchi,

Parurios Girault, *Pondia* Hedqvist, and *Pseudipara* Girault under *Dipara* Walker;

Spalangiolelaps Girault under *Lelaps* Walker; *Australolaelaps* Girault under

Neapterolelaps Girault; *Dolichodipara* Hedqvist under *Myrmicolelaps* Hedqvist; and

Dipareta Boucek and *Malinka* Boucek under *Pseudoceraphron* Dodd, **new synonymies**.

Three genera are described as new: *Cerodipara*, *Dozodipara*, and *Noortia*. Fourteen new

species are described: *Cerodipara sabensis*, *Chimaerolelaps villosa*, *Conophorisca*

littoriticus, *C. grisselli*, *Dozodipara insularis*, *Lelaps noorti*, *Myrmicolelaps iridius*, *M.*

aurantius, *Neapterolelaps viridescens*, *N. mitteri*, *Nosodipara ferrana*, *Pseudoceraphron*

regieri, *P. burwelli*, and *P. fijensis*. A key to the genera of Diparinae is provided. The

species of each genus are cataloged, and species-level keys are provided for most genera

in which new species are described. New biological information shows that diparine host

range is not restricted to Curculionidae as previously thought; one species of

Myrmicolelaps were reared from mantid oothecae and a second from a tsetse fly

puparium (Glossinidae: *Glossina*).

Introduction

Chalcidoidea, one of the largest superfamilies of parasitic Hymenoptera, includes about 22,000 described species (Noyes 2003). The majority of chalcidoids, commonly called chalcids, are parasitoids and have major importance in the biological control of insect pests. Despite the ecological and economic importance of Chalcidoidea, phylogenetic relationships both within and between chalcidoid families are still largely obscure. A central difficulty is the status of the problematic family Pteromalidae, one of the three largest (3506 species (Noyes 2003)) and often considered the "garbage can" of the superfamily. Pteromalidae is defined only by the absence of features defining other chalcidoid families and may be paraphyletic with respect to a number of these; the limits and placement of this family are simply unknown. Thirty-one subfamilies are currently recognized within Pteromalidae (Noyes 2003), although inclusion and exclusion of many subfamilies is still highly uncertain. Few comprehensive phylogenetic studies have been conducted at the subfamily or tribal level (see Heydon 1997, Gibson 2003 for examples), making the coding of characters and choice of exemplars difficult in higher-level analyses.

One of the most enigmatic of pteromalid subfamilies is the Diparinae. Because the diparines are aberrant in habitat (leaf litter on the forest floor) and habitus (most females being wingless), they are rarely collected even by chalcidologists, and their taxonomy and life history are mostly unknown. The only known host record was recorded by Boucek (1988), in which *Parurios sp.* was reared from a curculionid (Coleoptera). A world revision of the diparines has never been published, and identication of genera is difficult even with access to the primary literature and a

representative collection. Recent morphological work has hypothesized sister-group

relationships of other pteromalid subfamilies with diparines (Darling 1988, 1991a; Török

and Abraham 2001), particularly Ceinae, thus making improved systematics of these

obscure wasps important to testing these conclusions. This study therefore includes a

morphological phylogeny and revision of the genera of the world Diparinae. The aim of

the phylogenetic analysis is three-fold: 1) to establish monophyly (or non-monophyly) of

Diparinae, 2) to construct a phylogeny of the genera, and 3) to test the proposed sister-

group relationship with Ceinae.

Diparinae historically consists of 117 species distributed throughout 31 genera

(Noyes 2003), but examination of museum collections has revealed a tremendous number

of undescribed species. The tribal classification has been unstable and has often changed

with each regional revision. Many of the genera are monotypic and are described from

small series or even single specimens (e.g., Hedqvist 1969). Of the 31 genera, 24 contain

two or fewer species, while only five contain five or more species. Even now many of

the genera are known only from type specimens. The group has never been revised on a

world basis and few regional revisions exist. The small faunas of the Nearctic

(Yoshimoto 1977) and Western Europe (Graham 1969) have been revised and keyed

recently, although they account for only a small portion of diparine diversity. Hedqvist

(1969) revised and keyed the African fauna, while Boucek (1988) revised and provided a

key to the Australasian genera. However, more extensive sampling in both the

Afrotropical and Australasian regions has revealed many undescribed species that require

the alteration of generic concepts.

Diparines are often noted for their marked sexual dimorphism. The majority of known males are macropterous, have filiform antennae, and show little to moderate variation between genera. Females may be macropterous, brachypterous, or even apterous, often have clavate antennae, and display great morphological variation across genera. Some females have such bizarre morphological forms that even taxonomists may have difficulty identifying them as chalcidoids (e.g., *Pseudoceraphron* Dodd was originally described in the Ceraphonidae (Ceraphronoidea; Dodd 1924). As most species and many genera are described solely from either males or females, the lack of host records and successful rearings suggest that many currently distinguished genera and species might actually represent males versus females of single or congeneric species. It is possible that caged live-caught diparine females could be used to attract mates and associate the sexes, a technique applied successfully to other female-wingless Hymenoptera (e.g., Mutillidae; Manley 1999). However, the difficulty of capturing live females locally precluded attempting this methodology over the course of this study.

Overall the Diparinae have a cosmopolitan distribution and are generally most common in lowland and montane rainforests. Diparines appear to have a Gondwanan center of diversity, being most diverse at the generic level in South Africa and Australia. In Australia, most diparine diversity is restricted to Queensland and the surrounding islands. To a lesser extent they are distributed throughout Western Australia, southeastern Australia, and Tasmania, particularly *Netomocera* Boucek and *Liepara* Boucek which are generally found in drier forests and arid regions. In Africa, most genera are known only from South Africa, although this may be an artifact of intensive sampling (both from the R.E. Turner collection and recent collecting by S. van Noort,

Cape Town Museum). Small collections from Namibia, Botswana, Zimbabwe, Tanzania, and Kenya suggest that this diversity extends farther north, particularly through the East Rift Valley. Oddly, while the diversity of diparines in most regions seems to be highest in the rainforest, this is exactly the opposite in southern and eastern Africa, where the distribution of the rainforest coincides with a dramatic drop in diparine generic diversity. The majority of southern and eastern African genera exist in drier areas, including the fynbos, savannah, and montane grasslands.

It is unknown whether this Gondwanan pattern of diversity extends into southern South America where no endemic genera are known, although this may be an artifact of limited collecting in those areas. In the New World, diparines are genera-poor, the only endemic genera being *Lelaps* and the newly described *Chimaerolelaps* (neither of which have a distribution which extends into southern South America). However, *Lelaps* is possibly the most speciose genus in Diparinae, containing 40 described and a great number of undescribed species. Southeast Asia and the Congo Basin region of Africa show a similar pattern of genera-poor, species-rich diversity, where *Dipara* species make up the majority of diparine diversity in these areas, and no endemic genera are known.

Methods

Collecting Methodology

Diparines are poorly represented in most museum chalcidoid collections, especially wingless females which generally inhabit litter environments. Malaise traps and sweeping, typically used for collecting chalcidoids, generally yield only winged males. The primary exception to this is *Lelaps* in the Neotropics, where the winged females characteristic of many species can be collected using these methods. Yellow pan traps, and to a lesser extent flight-intercept traps, are effective methods of collecting both diparine sexes. For a detailed discussion of these and other collecting methods, see Noyes (1982). Another effective method of collecting diparines is a modified pyrethrum knockdown technique developed by Geoff Monteith of the Queensland Museum (Brisbane, Australia). A smooth, plastic sheet is first placed below a rotten log, tree trunk, exposed tree roots, or other desired collecting area. Then the log surface is sprayed with a fast-knockdown pyrethroid insecticide. A short time is then allowed for insects to emerge, die, and fall onto the plastic sheet below. The sheet can then be funneled into a vial of ethanol or other desired collecting media. Although this technique has thus far only been used to collect diparines in Australia and surrounding islands, it has proven quite effective in those regions and shows promise for use in other areas.

Terminology

All taxonomic names stated in this paper refer to the classification scheme provided here unless referred to in the sense of an author. *Dipara* in particular is referred to in two different ways: *Dipara*, which refers to *Dipara* as defined here and includes the new synonyms *Alloterra* Kieffer and Marshall, *Diparomorpha* Hedqvist, *Grahamisia* Delucchi, *Parurios* Girault, and *Pseudipara* Girault; and *Dipara sensu* Boucek (1988). Taxonomic units in the phylogenetic analysis are listed as they are classified here, following by their tradition classification or OTU in parentheses [e.g., *Dipara* (*Alloterra*)]. In some instances, Diparinae is referred to as Diparinae excluding *Liepara* for the purpose of clarification; both terms as presented here have the same meaning.

Morphological terminology follows that of Gibson (1997) unless otherwise noted. A **seta** (e.g., Fig. 29) is short, thin, and usually light in coloration, while a **bristle** (e.g., Figs. 18-20) is long, thick, and usually black in coloration. Setae are considered **sparse** (e.g., Fig. 29) if each seta is separated from other seta by at least its own length. Although the lower face is defined in Gibson (1997) to include the clypeus, when referred to here it does not. The ventral margin of the face is therefore the edge between the clypeus and the gena. The **posterior notal wing process** (apparent in Figs. 20, 50, 51) is a sclerotized projection emerging from the lateral margin of the scutellum between the fore- and hindwing. In the genus *Myrmicolelaps*, an **axillary wing sclerite** (Fig. 30) is expanded and visible posterior to the tegula. The **cercal brush** (Figs. 13, 17, 35) is a dense patch or line of short, white setae, facing posteriorly, just anterior to the cercus itself. The setae themselves point posteriorly. It can be difficult to see in some specimens and is most visible when viewed from an antero-lateral angle. Surface

sculpture terminology follows that of Harris (1979) unless otherwise stated in the description.

Museum Abbreviations

The following is a list of museum abbreviations used in the taxonomic revision. For the most part these abbreviations are based on Arnett *et al.* (1993), which is updated and maintained at the Bishop Museum (Honolulu, Hawaii, USA) website (http://hbs.bishopmuseum.org/codens/codens-r-us.html). Collection abbreviations marked with an asterisk were not listed on the website.

AEIC   American Entomological Institute, Gainsville, Florida, USA

ANIC   Australian National Insect Collection, Canberra, Australia

BPBM   Bishop Museum, Honalulu, Hawaii, USA

BMNH   British Museum of Natural History, London

CNC   Canadian National Collection, Ottawa, Canada

DZCU   Calcutta University, Calcutta, India

DPC*   Delucchi Private Collection

FSCA   Florida State Collection of Arthropods, Gainesville, Florida, USA

KHPC*   Karl-Johan Hedqvist Private Collection

MDLA   Laboratório de Biologia, Dundo, Lunda, Angola

MHNG   Museum d'Histoire Naturelle, Geneva, Switzerland

MRAC   Musée Royal de l'Afrique Centrale, Tervuren, Belgium

NHRS   Naturhistoriska Riksmuseet, Stockholm, Sweden

NMPC	National Museum (Natural History), Prague, Czech Republic
PPRI	Plant Protection Research Institute, Pretoria, South Africa
QM	Queensland Museum, Brisbane, Australia
SAM	South Australian Museum, Adelaide, Australia
SAMC	South African Museum, Cape Town, South Africa
UCDC	University of California, Davis, California, USA
USNM	United States National Museum, Washington, DC, USA
ZMHB	Zool. Mus. der Humboldt - Universität zu Berlin

Phylogenetics of Diparinae

Taxonomic Scope

A preliminary examination of the genera of Diparinae was conducted in order to remove taxa which obviously belonged to other groups or which could not be coded for a sufficient number of characters. A large number of diparine genera were described in the early 1900's, when classification of Chalcidoidea was still in its early stages. Since Diparinae has never been revised on a world level, many genera traditionally classified within the group have obvious affinities to other subfamilies but have never been removed from Diparinae. These taxa were removed prior to the phylogenetic analysis because many of the characters used in the matrix had little relevance to these taxa. Taxa which were removed from the analysis because of insufficient coding were generally known only from males (making it impossible to code them for the large number of female-only characters), or in one case the type material was not located.

Specifically, *Bekilliela* Risbec and *Dinarmolaelaps* Masi were excluded from the analysis because neither are diparines (their taxonomic placement is discussed in their generic entries), and both genera are known only from males. *Seyrigina* Risbec was excluded from the analysis because it belongs in Eulophidae and it known only from the holotype, of which both the head and gaster are missing. *Diparomorpha* Hedqvist does belong in Diparinae, but was excluded from the analysis because it is known only from the holotype, which could not be located, and the description did not provide enough information to code the genus for a sufficient number of characters. The placement of *Diparomorpha* is discussed further in the generic entry for *Dipara*. The four Hawaiian

genera (*Calolelaps* Timberlake, *Mesolelaps* Ashmead, *Neolelaps* Ashmead, and *Stictolelaps* Timberlake) were coded in the matrix but excluded from the analysis, because after coding they were determined to belong in Miscogasterinae and also to reduce the taxon:character ratio in the phylogenetic analysis.

For the most part, taxonomic units in the data matrix were genera. Exceptions to this were clades of genera in which a large number of undescribed species did not fit into the historical generic concepts (*Australolaelaps* and *Neapterolelaps*; *Dipareta*, *Malinka*, *Nosodipara*, and *Pseudoceraphron*; and *Conophorisca*, *Dolichodipara*, and *Myrmicolelaps*). New species were described to better understand phylogenetic relationships within those groups, and most described species were included in the analysis (*Neapterolelaps* was coded as a single generic unit). Additionally, *Dipara sensu* Boucek (1988) was divided into multiple taxonomic units to better resolve its relationships with *Alloterra*, *Grahamisia*, *Parurios*, and *Pseudipara*. These divisions were based on groups which could be coded relatively unequivocally in the data matrix, as the variation within *Dipara sensu* Boucek (1988) made the coding of too many characters ambiguous. Additionally, separating *Dipara sensu* Boucek (1988) from *Parurios* on a world level proved impossible given the definitions of both genera. Additional species of *Dipara* were not described due to both time constraints and the sheer number of species which would need to be described to thoroughly examine this group.

The subdivisions of *Dipara sensu* Boucek (1988) include:

- *Dipara turneri* Hedqvist, a species from Africa which appears to lie between *Dipara* and *Parurios* morphologically;

- "Fijian *Dipara/Parurios*," an unclassifiable species from Fiji which shares some features with *Dipara turneri*;

- "Indonesian *Pondia*," a group of undescribed, *Dipara*-like species known from Indonesia and Taiwan, which are often identified as *Pondia* in museum collections due to their convex scutellum;

- "Australian *Dipara*," Girault's Australian genera (*Epilelaps* and *Pseudiparella*) which Boucek (1988) synonomized with *Dipara*;

- "Micro *Dipara*," generally minute, macropterous species of *Dipara sensu* Boucek (1988) with collar-like pronota;

- *Dipara sensu stricto*, which are generally apterous, have a laterally bulging pronotum, and include the most well-known members of the genus (e.g., *D. canadensis*).

Outgroups selected included all three genera of Ceinae, and two representatives each from Eunotinae and Coelocybinae. Ceinae was thoroughly represented because Darling (1991a) proposed a sister-group relationship between Ceinae and Diparinae based on two morphological features: the presence of admarginal setae and papilliform antennal sensillae. Additionally, in a morphological study of Pteromalidae by Török and Abraham (2001), Ceinae grouped as sister to Diparinae in their reweighted parsimony tree with all taxa included. *Bohpa* Darling (Ceinae) was coded for all characters and analyses were run both including and excluding this taxa for three reasons. First, the

male of *Bohpa* is unknown. With a wingless female and unknown male, it is impossible to code *Bohpa* for many of the characters important at the base of the phylogeny, including presence/absence of admarginal setae and the number of anelli in the male. Second, the addition of a third ceine genus does little to polarize characters within the clade, as among three taxa a gain and a loss are equally as parsimonious as two independent gains of a character state. Third, the inclusion of *Bohpa* in the analysis dramatically impacted the successive weighting of characters important to the phylogeny the derived diparines, which is discussed below. Eunotinae and Coelocybinae were chosen as additional outgroups based in discussions with other chalcidologists about which subfamilies might be closely related to Diparinae.

Character Coding

When possible, all characters, unless noted as "male", were taken from female specimens. If a female specimen was unavailable, or the character of interest was damaged on all female specimens but visible on a male, the character was coded from the male. Exceptions to this are noted as (female), in which case sexual dimorphism causes females to have distinctive morphology from males for this character. Taxa coded with "(#)" are polymorphic for that character, i.e. different species in the taxonomic unit have distinctly different states. Taxa coded with "{#}" are ambiguous for that character, i.e. the state present in the taxon is intermediate between multiple coded states. Coding for all taxa is listed in Appendix I.

One of the features typically used to diagnose Diparinae is the presence of strong, dark bristles on the vertex and dorsal surface of the mesosoma. During the course of

character coding for this analysis, it was noticed that although many diparines have a varying numbers of bristles, they always had bristles positionally identical to a subset of the full complement of bristles. To utilize this positional homology information in the phylogenetic analysis, bristles were coded in the following way: First, a single character for overall presence or absence of bristles was coded for all taxa (i.e., every taxon with at least 1 pair of bristles was coded as present, #21). Second, an additional presence/absence character was coded for each positionally homologous pair of bristles (#22-24, 26-29), as was a final additional character on the position of the median scutal bristle pair (#25). All bristle positional characters were coded as missing (?) if overall bristle presence/absence was coded as absent. This was intended not to give a disproportionate amount of weight to the presence/absence of bristles, as it is plausible that all bristles could be lost in a single evolutionary step.

Two issues arise from this coding scheme, however. First, by coding positional bristle characters for all taxa without an overall presence/absence character, the large number of bristle characters themselves could drive much of the phylogenetic signal in the tree if they supported the same groupings. Second, strange step requirements can occur when reconstructing character states. For example, a taxon without bristles can be reconstructed as sister-group to a taxon with all bristle pairs with a single step (overall bristle presence/absence). To then place a taxon with a single bristle pair within that clade as sister to the bristleless taxon would require at least 6 additional steps, while this transformation seemingly should only take 1 step. A character could be constructed in which all possible bristle conformations are coded as different states (which was done with notaular shape), but the vast number of potential states would prove uninformative

in the analysis. Therefore, analyses were run both including and excluding positional bristle characters.

Additionally, the form of the notauli was originally coded as multiple characters (#32-35). However, notauli appear to be highly divergent in closely related taxa, and having multiple characters would imply a heavy weighting. In order to minimize the effect of notauli on tree topology, characters #32-34 were combined into a single character representing all possible arrangements of the notauli (#31), and characters #32-34 were excluded from all analyses. Character #35 (notaular pads) was left as is, because, although the black pads are located adjacent to the notauli but not innately part of notaular structure.

1. Apical Clypeal Margin: 0 = concave (Fig. 45); 1 = with median tooth or lobe (Fig. 16); 2 = protruding, symmetrically bilobed (lobes may be very small and appear symmetrically sinuate); 3 = convex, or protruding and straight.

A convex clypeal margin is coded the same as a protruding clypeus with a straight margin, as the blurring between these two forms makes them difficult to code as separate. Additionally, both lack the lobes or teeth of states 1 or 2, and project from the ventral margin of the head, as opposed to state 0. The clypeal margin has not been previously used in diparine taxonomy, with the exception of *Lelaps* and *Spalangiolaelaps*, which are often partially diagnosed by a median tooth (e.g., Yoshimoto 1977). In his phylogenetic analysis of Toryminae, Grissell (1995) used a more finely detailed transformation series of the clypeal apex, which was highly consistent within the phylogeny (CI = 1.00).

2. Posterior Margin of Gena: 0 = smooth; 1 = carinate.

Outside of Diparinae, a carinate genal margin is found sporadically in Chalcididae (Wijesekara 1997), Eucharitidae (Heraty 2002), and also in Eurytomidae and New World Lyscini (Pteromalidae: Cleonyminae) (Gibson 2003). Gibson (2003) states that this feature is often associated "with a head that is closely appressed to the pronotum so the two form a more rigid association."

3. Dorsal Margin of Scrobe: 0 = rounded; 1 = carinate.

This character is sporadically distributed throughout Diparinae. The presence of a carinate dorsal margin is probably correlated with the overall "carinateness" of a chalcidoid, i.e. diparines which are heavily sculptured often have carinate margins of many features.

4. Scrobe Shape: 0 = scrobe present and scrobal channel parallel-sided (Figs. 7, 27), 1 = scrobe present and scrobal channel wide, triangular dorsal to toruli (Fig. 36), 2 = wide, shallow depression, scrobe basically absent (Fig. 44), 3 = scrobe distinct and short, but without scrobal channel (Fig. 52), 4 = scrobe triangular and wide, but without scrobal channel.

State 3 is autapomorphic for *Pondia*. Gibson coded a similar character in his cleonymine (2003) and eupelmid (1989) phylogenetic analyses. In both groups he found that most members possessed scrobes with distinct scrobal channels (equivalent to state 0 in this analysis), although the scrobes had been reduced or lost in some members of both groups.

5. Occipital Margin: 0 = rounded; 1 = carinate.

The occipital margin refers to the boundary between the posterior margin of the vertex and the dorsal margin of the occiput.

6. Occipital Carina: 0 = absent; 1 = present.

The presence of an occipital carina was initially coded as two separate states, one in which the carina was visible only as line dorsal to the occipital foramen, and another where the carina was a semicircular line, laterally reaching ventral to the occipital foramen. However, the ambiguity in coding this character for many taxa has led to the reduction the presence of the occipital carina to a single state. Grissell (1995) hypothesized that the absence of an occipital carina is the ancestral state in Pteromalidae, as did Gibson (2003) regarding Cleonyminae.

7. Face Sculpture (female): 0 = Upper face without strong, transversely carinate sculpture (Figs. 7, 27, 36, 44); 1= Upper face with deep pits separated by strong transverse carinae.

This feature is unique to *Dipara turneri* and "Fijian *Dipara/Parurios*", and was included to help discern the internal phylogeny of the *Dipara* clade. As the males of both these species are unknown, it is uncertain whether or not this sculpture is present in both sexes, and the character is therefore only coded from females.

8. Torular Shelf : 0 = toruli not on shelf, either with sharp angle of 45° or less between upper face and lower face, or junction between upper and lower face rounded (Fig. 20), 1 = toruli on shelf, sharp angle of ~90° between upper and lower face (Fig. 8).

9. Malar Groove: 0 = present; 1 = absent.

   The malar groove of *Dolichodipara iridius* is coded as ?, because although there is no distinct line, a depressed area delimited by a change in sculpture marks the location of the malar groove. This character may not be independent from body size, as the malar groove tends to lost in the most diminutive taxa.

10. Posterior Eye Extension: 0 = normal, eye not extending posteriorly beyond occipital margin, pronotum visible in lateral view (Fig. 20); 1 = eye extended posteriorly beyond occipital margin, laterally obscuring pronotum.

   This character is exists to a varying degree in the eunotines *Eunotus* and *Moranila*, and is coded as polymorphic for both taxa.

11. Inner Eye Margins: 0 = parallel-sided or uniformly convex; 1 = ventrally diverging.

   This character has historically been used to help define the outgroup Coelocybinae (e.g., Boucek 1988) as well as Eupelmidae (Gibson 1989). Gibson (2003) found that diverging inner eye margins supported monophyly of Cleonyminae if the outgroup Hetreulophini (Colotrechninae) was excluded from the analysis and his interpretation of the character in *Callimomoides* was incorrect. However, Gibson did not include representatives of Eupelmidae and Coelocybinae in his analysis, which casts

further doubt on the utility of this character for defining Cleonyminae. Regardless, due to the uniformity of distribution of this feature in pteromalid subfamilies and Eupelmidae, it may become an important character in the higher phylogeny of Chalcidoidea. Within the Diparinae, ventrally diverging eyes are unique to *Cerodipara*.

12. Eye Setae: 0 = eyes bare; 1 = eyes sparsely setose.

Eyes are only coded as setose if the setae are readily visible under microscopic examination. If the setae are so small and sparse as to only be visible at certain angles of light and high magnification, they are considered bare. Unforunately, a vast majority of diparines fall into this latter category, and the coding of this character may be heavily influenced by personal interpretation. Eye setation appears fairly variable within Diparinae, and shows a similar pattern of variability in both Cleonyminae (Gibson 2003) and Eupelmidae (Gibson 1989, 1995).

13. Antennal Shape (Female): 0 = filiform; 1 = clavate; 2 = clubbed.

14. Antennal Symmetry (Female): 0 = symmetrical; 1 = asymmetrical.

An asymmetrical flagellum is one of the diagnostic characters of Coelocybinae (Boucek 1988). Within Diparinae, an asymmetrical flagellum is unique to *Netomocera*.

15. Anellar Number (Female): 0 = 1 anellus; 1 = 2 anelli; 2 = 3 anelli; 3 = 5 anelli; 4 = 7 anelli.

In cases where the anellus is partially fused to the first funicular segment (e.g. *Myrmicolelaps aurantius*, see Fig. 26), these taxa are coded as having a single anellus.

16. Flagellar Number (Female): 0 = 11 flagellar segments (counting clava as 3); 1 = 8 or fewer flagellar segments (counting clava as 3).

A reduced number of flagellar segments is often used as a diagnostic feature of Eunotinae (e.g., Boucek 1988).

17. Pedicel:F1 (Female): 0 = first funicular segment subequal in length to pedicel; 1 = first funicular segment at least 1.5X as long as pedicel; 2 = pedicel at least 1.5X as long as first funicular segment.

Taxa between states (e.g., pedicel 1.3X as long as F1) were coded as ambiguous. Gibson *et. al* (1997) used a version of this character "first funicular segment longer than pedicel" in their generic key for separating *Lelaps* and *Spalangiolelaps* from other Nearctic genera (and more easily than the F1:F2 character used by Yoshimoto (1977)). However, this character does not separate *Lelaps* and *Spalangiolelaps* from many other non-Nearctic diparines.

18. F1:F2 (Female): 0 = First funicular segment subequal in length to second funicular segment; 1 = First funicular segment at least 1.5X longer than second funicular segment.

All species of *Pseudoceraphron* are coded as N/A for this character, because they have 7 anelli and only a single funicular segment. Yoshimoto (1977) used an elongate F1 to define the tribe Lelapini (*Lelaps* and *Spalangiolelaps*) in his key. *Nosodipara ferrana*

also has F1 at least 1.5X longer than F2, although this is due to a shortened F2 rather than an elongate F1.

19. Claval Fusion (Female): 0 = clava 3-segmented (Figs. 15, 43); 1 = clava 2-segmented, distal 2 segments apparently fused; 2 = clava 1-segmented, all segments apparently fused (Figs. 5, 6, 25).

A two-segmented clava is autapomorphic for *Conodipara*. Gibson (2003) used a similar coding in his phylogenetic analysis of Cleonyminae (2003). This character appears to show a moderate degree of variability in both the Cleonyminae (Gibson 2003) and Eupelmidae (Gibson 1989).

20. Claval Micropilosity (Female): 0 = clava without thick tuft of micropilosity on apex of clava (Figs. 5, 6, 15, 25, 36); 1 = clava with thick tuft of micropilosity on apex of clava (Figs. 42, 43).

The micropilosity at the apex of the clava of *Pseudoceraphron* and *Nosodipara* appear to be sensillae rather than setae. In Figure 43, it can be seen that the dorsal sensillae appear to have closed, rounded tops, while the ventral sensillae appear to have open, truncated tops. It is possible that the tips of the ventral sensillae were sheered off during SEM preparation. However, the uniformity of the open-topped sensillae suggests that is unlikely.

21. Bristles (Presence/Absence): 0 =without any strong, dark bristles on the thorax or vertex, excluding bristles emanating from the wing stump in apterous specimens; 1 = at

least 1 pair of strong, dark bristles present on the thorax or vertex, excluding bristles emanating from the wing stump in apterous specimens.

Strong, dark bristles are used by many keys to diagnose Diparinae (e.g. Boucek 1988, Gibson et. al. 1997), although many diparine genera lack bristles completely.

22. Bristles (Vertex): 0 = absent; 1 = bristle pairs limited to occipital margin and dorsal inner eye margins (Fig. 18); 2 = bristles uniformly distributed across vertex; 3 = with only a single pair of bristles posterior to the lateral ocelli.

Not only do the bristle patterns differ fundamentally between states 1 and 2, but the bristles of *Lelapsomorpha* are significantly thinner than most taxa having state 1 (although this difference was too difficult to code, and may not be entirely independent from the pattern itself). State 3 is unique to *Chimaerolelaps*.

23. Bristles (Pronotal): 0 = without bristles on pronotum; 1 = with transverse row of bristles on pronotum; 2 = with a single pair of bristles on prontum.

24. Bristles (Medial Scutal): 0 = without pair of bristles on scutum medial to notauli; 1 = with a single pair of bristles on scutum medial to notauli; 2 = with two pairs of bristles on scutum medial to notauli.

State 2 is unique to *Moranila*.

25. Position of Median Scutal Bristles: 0 = normal, distance from scuto-scutellar margin to median scutal bristles longer than distance to anterior scutellar bristles; 1 =

short, distance from scuto-scutellar margin to median scutellar bristles shorter than distance to anterior scutellar bristles.

Boucek (1988) used this character to separate female *Dipara* and *Parurios* in his key, although he stated that non-Australian *Dipara* would key to *Parurios* using this feature (therefore it will separate Australian *Dipara* from the remainder of the *Dipara s. l.* clade). This character is only coded in taxa which have both A) median scutal bristles, and B) a single pair of anterior scutellar bristles. All other taxa are coded as N/A.

26. Bristles (Lateral Scutal): 0 = without bristles on lateral lobes of scutum; 1 = with a single pair of bristles on the dorso-lateral margin of the lateral lobes of scutum (Fig. 19); 2= with a single pair of bristles on the antero-medial portion of the lateral lobes of scutum (Fig. 22); 3 = with two pairs of bristles on lateral lobes of scutum.

States 2 and 3 are possessed only by outgroup taxa. *Moranila* possesses a single pair of bristles which is not positionally homologous to those in the Diparinae, while *Lelapsomorpha* and some species of *Spalangiopelta* both possess two pairs of lateral scutal bristles.

27. Bristles (Anterior Scutellar): 0 = without pair of bristles on anterior half of scutellum; 1 = with a single pair of bristles on anterior half of scutellum; 2 = with two pairs of bristles on the anterior half of scutum.

Two pairs of anterior scutellar bristles is unique to both *Lelapsomorpha* and *Chimaerolelaps*.

28. Bristles (Posterior Scutellum): 0 = without pair of bristles on posterior half of scutellum; 1 = with pair of bristles on posterior half of scutellum, either at posterior margin (if frenum is absent) or lateral margins of frenal line (if frenum is present); 2 = with pair of bristles on posterior half of scutellum, posterior to distinct frenal line.

State 2 is autapomorphic for some species of *Spalangiopelta*.

29. Bristles (Propodeal): 0 = without pair of bristles on propodeum; 1 = with pair of bristles on lateral margins of propodeum.

Propodeal bristles are unique to *Pseudoceraphron* (*Malinka*).

30. Pronotum Shape: 0 = short, collar-like, not dorsally or laterally bulging, and at least as wide as long (Fig. 19, 20,22, 46, 47, 48); 1 = large, laterally but not dorsally convex; 2 = large, both laterally and dorsally convex (Fig. 9); 3 = large, cylindrical, longer than wide.

31. Notauli (combined): 0 = notauli absent; 1 = notauli present only in anterior half; 2 = notauli complete, Y-shaped; 3 = notauli strongly arched along entire length (appearing semi-circular) and meeting posterior scutal margin at scutoscutellar suture; 4 = notauli not arched and meeting posterior scutal margin exterior to or at the edge of scutoscutellar suture; 5 = notauli strongly arched anteriorly and running parallel posteriorly, meeting posterior scutal margin at scutoscutellar suture; 6 = notauli not arched and meeting posterior scutal margin at scutoscutellar suture; 7 = notauli inverted, U-shaped, meeting anterior to posterior scutal margin.

32. Notauli: 0 = notauli distinct along their entire length; 1 = notauli faded posteriorly; 2 = notauli absent.

Gibson (2003) hypothesizes that distinct notauli are pleisiomorphic for the Cleonyminae, although the character varies within the group and also in eupelmids (Gibson 1989, 1995). Wijesekara (1997) coded all chalcidids as having distinct notauli, while they were completely absent in his leucospid outgroup. Grissell (1995) also hypothesized that distinct notauli were pleisiomorphic for Toryminae, although he also stated that the character was so homoplastic as to provide little information. Within the Diparinae only *Pyramidophoriella* lacks notauli completely.

33. Notaular Meeting: 0 = notauli posteriorly widely spaced, meeting posterior scutal margin exterior to or at the lateral edge of the scutoscutellar suture; 1 = notauli posteriorly narrowly spaced, meeting posterior scutal margin at scutoscutellar suture, or notauli meet at or just anterior to posterior scutal margin; 2 = notauli Y-shaped, meeting well anterior to posterior scutal margin.

Both Gibson (1989, 2003) and Grissell (1995) used similar characters. While Gibson (2003) found this character difficult to code for cleonymines, most eupelmids have notauli which are "distinctly exterior to the scutoscutellar suture" (= widely spaced in this analysis). Grissell (1995) coded all torymines as having widely spaced notauli except *Palachia*. Diparines with U-shaped notauli are coded as ambiguous for this character, as they often have extremely short scuta, making this difficult to code. *Pseudoceraphron* are coded as 0 for this character, as its notauli are widely spaced. The notauli do meet posterior scutal margin within the boundaries of the scutellum, but this is

because *Pseudoceraphron* has an extremely wide scutellum without axillae (and therefore no scutoscutellar suture).

34. Notaular Arch: 0 = notauli not arched, almost appearing as straight lines; 1 = notauli strongly arched along entire length, appearing semi-circular; 2 = notauli strongly arched anteriorly, but running parallel sided posteriorly; 3 = notauli U-shaped, arch inverted.

Diparines with Y-shaped notauli are coded as ambiguous for this character, as the short distance the notauli travel before meeting each other makes it difficult to code for this character.

35. Notaular Pads: 0 = lateral lobes of scutum without raised, black pads; 1 = lateral lobes of scutum with raised, black pads, lateral to the posterior central groove of Y-shaped notauli.

The presence of these notaular pads has been used to separate *Dipara* (*Grahamisia*) from *Dipara sensu* Boucek (1988), and *Pseudoceraphron* (*Malinka*) from both *Pseudoceraphron sensu* Boucek (1988) and *Pseudoceraphron* (*Dipareta*).

36. Posterior Scutal Margin: 0 = posterior scutal margin lateral to scutellum either not grooved or without cluster of setae (Figs. 10, 19, 22, 38, 48, 55); 1 = posterior scutal margin lateral to scutellum grooved for the insertion of the anterior margin of the tegula, with small cluster of setae on the medial edge of groove (Fig. 30).

37. Scutellum Shape (Female): 0 = large, convex, gently sloping down posteriorly (Figs. 19, 22, 50, 51); 1 = wider than long, sloping up and slightly pointed posteriorly (Figs. 37, 38); 2 = conical and tooth-like, narrowed anteriorly, slightly laterally compressed, and flattened posteriorly (Figs. 9, 11, 54, 55); 3 = small, strongly convex, not sloping posteriorly (Fig. 53); 4 = flat, wider than long (Fig. 48); 5 = square, slightly raised and laterally compressed medio-posteriorly (Fig. 29); 6 = large, slightly convex, not sloping posteriorly; 7 = slightly convex, wider than long, lateral and posterior margin with upturned carina (see Darling 1991b: Figs. 6, 9).

There is a tremendous amount of morphological variation in the diparine scutellum. State 1, 6, and 7 appear to autapomorphic for *Neapterolelaps*, *Dozodipara*, and *Bohpa*, respectively. *Dipara turneri* is coded as state 0; although its scutellum is slightly flattened, it is still large and slightly convex.

38. Axillae (Female): 0 = normal, large and convex (Figs. 19, 22, 50, 51); 1 = reduced and convex (Fig. 38); 2 = reduced and concave or flat (Figs. 10, 29); 3 = entirely absent (Fig. 48); 4 = indistinct from scutellum, indicated only by faint sulcus between axilla and scutellum (see Darling 1991b: Figs. 1, 3).

State 4 is autapomorphic for *Bohpa*.

39. Posterior Notal Wing Process (Female): 0 = present, pointed (Figs. 19, 22, 50, 51); 1 = absent (Figs. 29, 46, 47); 2 = present but squarely truncate (Fig. 38); 3 = present but truncate and rounded.

Many apterous diparines have a reduced or absent posterior notal wing process. This character may be an accurate measure of "potential" wing size, as taxa with both apterous and macropterous members have complete posterior notal wing processes even in their apterous members. State 2 is autapomorphic for *Neapterolelaps*.

40. Frenum: 0 = present; 1 = absent.

This character has been previously used to distinguish *Lelaps* (*Spalangiolaelaps*) (frenum absent) from *Lelaps* (frenum present). Grissell (1995) used this character in his phylogenetic analysis of the Toryminae and found it to be extremely homoplastic. This character may not be entirely independent from scutellum shape, as taxa with conical scutella never possess a frenum.

41. Metanotum: 0 = normal, sculptured, narrow band (Figs. 20, 22, 50, 51, 53); 1= absent, or present only as smooth narrow strip (Figs. 10, 38, 48); 2 = smooth, high, and vertical.

42. Dorsellum: 0 = present as raised, convex medial region of metanotum; 1 = completely absent (Figs. 10, 19, 29, 38, 48, 50, 51, 55); 2 = modified into cup-like structure (Fig. 22).

Moranila (and the entire tribe of Moranilini) uniquely possesses a modified, cup-shaped dorsellum.

43. Propodeal Shape: 0 = propodeum normal, descending posteriorly in lateral view, but at least 1.5X longer than high (Figs. 19, 37, 50, 51); 1 = propodeum steeply descending posteriorly in lateral view, as long as high or higher than long; 2 = propodeum rising posteriorly from anterior margin for a least a portion of its length (Figs. 9, 10, 54, 55); propodeum dorsally flat in lateral view, wider than long in dorsal view (Figs. 46, 47); propodeum dorsally flat in lateral view, longer than wide in dorsal view (Fig. 28).

Propodeal height and length measurements are made from the median posterior margin of metanotum to the dorsal margin of propodeal foramen.

44. Propodeal Spine: 0 = without anterior or median spine (Figs. 9, 10, 19, 22, 28, 29, 37, 38, 48, 50, 51, 55); 1 = with anterior spine, sometimes with a median carina emanating posteriorly; 2 = with median spine with 4-6 carinae emanating from it.

This character is included to help in resolving the relationships between and within Dipara (*Parurios*) and *Dipara sensu* Boucek (1988). *Lelapsomorpha* is coded as ? for this character because it does have an anterior protrusion on its propodeum, however, the protrusion is wide and dorsally flat, and therefore difficult to code as a spine.

45. Plicae: 0 = absent, or present but propodeum not strongly depressed lateral to plicae; 1 = propodeum with longitudinal plicae, and propodeum strongly depressed lateral to plicae.

46. Postspiracular Area: 0 = normal, suture between postspiracular area and metapleuron diagonal (Figs. 28, 37, 54, 55); 1 = facing posteriorly, suture between postspiracular area and metapleuron vertical (Fig. 49).

47. Propodeal Foramen: 0 = normal, open in one plane (Fig. 49); 1 = hinge-like, open in two planes (posteriorly and ventrally) (Fig. 31).

The genera *Conophorisca* and *Myrmicolelaps* all possess a propodeal foramen which appears hinge-like (i.e. it appears as two parabolas abutting at right angles, opening both posteriorly and ventrally).

48. Prepectus Extension: 0 = reduced, not extending posteriorly to tegula (Figs. 46, 47, 54); 1 = elongate, extended posteriorly along lateral margin of scutum to anterior margin of tegula (Figs. 20, 37).

Conodipara, Conophorisca, and *Myrmicolelaps* all have a prepectus which comes close to but does not touch the tegula. All of these genera have extremely short scuta, and the reduced distance between the prepectus and the tegula is hypothesized to be the result of the scutal reduction rather than an extended prepectus. These genera are therefore coded as state 0.

49. Tegula Shape: 0 = normal, flap-like (Figs. 20, 28, 30, 37); 1 = extended anteriorly along underneath lateral margin of scutum (Figs. 46, 47, 54, 55).

50. Mesepisternal Depression: 0 = absent (Figs. 20, 28, 37, 54); 1 = present (Fig. 46).

In the genera *Nosodipara* and *Pseudoceraphron*, there is a black, cylindrical depression on the anterior margin of the mesepimeron, which is partially laterally concealed by the pronotum (although visible ventrally) in all species except *Nosodipara monteithorum*.

51. Acropleuron: 0 = normal (Figs. 20, 37, 46, 47); 1 = large, convex, broadly expanded along entire dorsal length of mesopleuron (Figs. 9, 10, 11, 28, 54, 55).

Pyramidophoriella has a large, convex acropleuron which is not expanded anteriorly and is coded as ambiguous.

52. Posterior Mesopleural Sculpture: 0 = mesepipleuron posterior to femoral depression smooth; 1 = mesepipleuron posterior to femoral depression sculptured.

Although variable and difficult to code in many taxa, this character is included because it was found to reliably separates typcial females of *Dipara* (*Parurios*) (smooth) from those of *Dipara s. s.* (rough). *Mesolelaps* and *Pyramidophoriella* have a strongly sculptured area surrounded by smooth areas, and are coded as ambiguous for this character.

53. Axillary Wing Sclerite: 0 = not visible; 1 = expanded, present as tegula-sized sclerite latero-posterior to mesowing bud (Fig. 30).

Myrmicolelaps paradoxus is unique in that the axillary wing sclerite is expanded and completely covers the mesowing bud.

54. Metatibial Spur Number: 0 = 2; 1 = 1.

It should be noted that the number of metatibial spurs in the *Conophorisca* + *Myrmicolelaps* clade is more variable than the taxa coded imply, as examination of undescribed species in the latter clade shows multiple reversals to 2 spurs. The number of metatibial spurs appears to have been reduced within many groups, including Cleonyminae (Gibson 2003), Toryminae (Grissell 1995), and Chalcididae (Wijesekara 1997).

55. Metatibial Spur Length: 0 = longest spur <1.5X as long as width of tibia at point of insertion (Figs. 32, 33); 1 = longest spur at least 2X as long as width of tibia at point of insertion (Fig. 98).

The longer metatibial spur in *Pseudoceraphron* (*Dipareta*) *regieri* is between 1.5-2X the width of the tibia, and is coded as ambiguous.

56. Metacoxal Striations: 0 = absent (Figs. 23, 49); 1 =present (Figs. 21, 28, 32, 54).

There are some genera in which different species have varying degrees of overall sculpture. In the case where many species in a single genus have strong, apparent striations and other have faint, less apparent strations, the taxon is coded 1 in this analysis.

57. Metacoxal Brush: 0 = absent (Figs. 21, 28, 32, 46, 54); 1 = present (Fig. 39).

A thick vertical brush of white setae is present on the posterior margin of the metacoxa in *Australolaelaps*, *Neapterolelaps*, and *Archaeolelaps*.

58. Metacoxal Shape: 0 = normal, posteriorly convex (Figs. 21, 23, 28, 32, 39, 54); 1 = laterally compressed, large concave surface facing posteriorly (Fig. 49).

59. Admarginal Setae (in winged forms): 0 = absent; 1 = present.

All winged Diparinae appear to possess longer than normal setae on the ventral surface of the forewing just posterior to the marginal vein. If the female is apterous, and the male is both known and winged, the taxon is coding according to the male. Darling (1991a) noted the presence of admarginal setae are also present in many eulophid genera.

60. Ratio of Marginal Vein to Stigmal Vein: 0 = marginal vein is less than 1.5X length of stigmal vein; 1 = marginal vein is greater than 3X length of stigmal vein.

61. Petiole Length (Female) : 0 = broader than long to 1.2X as long as broad; 1 = at least 2X longer than broad.

62. Petiole Shape: 0 = cylindrical, 1 = strongly constricted antero-ventrally (Figs. 11, 12, 34); 2= midway along petiole length, curves downward at a sharp angle.

State 2 is autapomorphic for *Conodipara*.

63. Petiolar Setal Pairs (Female): 0 = petiole without setae (Figs. 11, 12, 34); 1 = petiole with 1 to 4 pairs of lateral or dorso-lateral setae; 2 = petiole with single pair of strong, dark bristles (Fig. 53).

State 2 is autapomorphic for *Pondia*. This state is added here instead of as a bristle character for two reasons. First, a unique bristle character for *Pondia* is autapomorphic and would be phylogenetically uninformative, and second, the bristle pair in *Pondia* is positionally homologous to the setal pairs in other taxa coded as state 1.

64. Petiolar Setal Tufts (Male): 0 = petiole without tufts of setae; 1 = petiole with lateral tufts of thick, white setae, at least in anterior half.

In *Archaeolelaps*, the tuft is present only along the anterior half of the petiole, while in *Neapterolelaps* it is present along the entire length of the petiole.

65. GT1 Constriction: 0 = GT1 rounded or straight lateral to petiolar insertion (Fig. 12); 1 = GT1 dorso-ventrally constricted lateral to petiolar insertion.

66. GT1 Size: 0 = normal, covering less than a quarter of the distance from anterior margin of gaster to anterior margin of cercus; 1 = expanded, covering at least half of the distance from anterior margin of gaster to anterior margin of cercus (Figs. 12, 34).

Within Diparinae only *Pyramidophoriella* lacks an expanded GT1.

67. Setal Tufts on GT1: 0 = absent (Figs. 11, 12, 19, 34); 1 = present (Figs. 37, 50, 51).

When present, thicks tufts of long, white setae are present on the anterior surface of GT1 just lateral to the petiole.

68. Cercal Form: 0 = exerted, digitform, 1 = flat, plate-like.

Gibson (20003) coded most cleonymines as having plate-like cerci, although the hypothetically primitive genera *Bouckekius* and *Chalcidiscelis* have digitiform cerci. Digitiform cerci have also been recorded in *Archaeopelma* (Eupelmidae) (Gibson 1989), female Torymidae, Agaonidae *s. l.*, and Chromeurytominae (Pteromalidae) (Grissell 1995).

69. Cercal Setae: 0 = short; 1 = long (Fig. 13, 17, 24, 34, 35, 41).

70. Cercal Brush: 0 = absent (Fig. 24); 1 = present (Figs. 13, 17, 34, 35, 41).

The cercal brush is a dense patch of setae abutting the anterior rim of the cercus (see Methods section).

71. Sexual Dimorphism: 0 = absent; 1 = present.

Minor differences in metasomal and antennal shape are not coded as dimorphism. *Conodipara, Conophorisca*, and *Myrmicolelaps* were all coded as absent for this character. However, rather than possessing generalized females and males as *Liepara* and the outgroup taxa do, these African genera have males which resemble the specialized wingless females typical of diparines. However, as this involves speculation, the original coding was kept.

72. Flagellar Segments (Male): 0 = flagellar segments cylindrical and short, at most 1.5X as long as wide; 1 = flagellar segments cylindrical and long, at least 1.5X as long as wide; 2 = flagellar segments pedunculate and long, at least 1.5X as long as wide.

This character is coded only for sexually dimorphic genera with known males, so as not to add weight to the sexual dimorphism character itself.

73. Flagellar Setae (Male): 0 = male antennae with short setae; 1 = male antennae with long, erect setae; 2 = male antennae with long, apically appressed setae.

As with the previous character, this character is coded only for sexually dimorphic genera with known males.

74. Number of Anelli (Male): 0 = 1 anellus; 1 = 3 anelli.

This character is included in addition to sexual dimorphism because *Spalangiopelta* is sexually dimorphic and the male has 3 anelli, whereas in sexually dimorphic diparines, the male has only a single anellus regardless of the female. Characters #74-76 may appear out of order in a morphological sense. This is because they were added to the matrix after the initial matrix was completed to further elucidate the relationship between Ceinae and Diparinae.

75. Claval Peg-Like Sensillae: 0 = absent; 1 = present.

This character was identified by Darling (1991b) as a potential synapomorphy for Ceinae, although the genus *Bohpa* (Darling 1991b) does not possess them.

76. Torular Position: 0 = antennal toruli separated from oral fossa by a distance of less than 1 torulus diameter; 1 = antennal toruli separated from oral fossa by a distance of greater than 2 torulus diameters (Figs. 8, 16, 27, 36, 44).

Phylogenetic Methodology

Parsimony analyses were performed using PAUP* version 4 (Swofford 1999). All characters were treated as unordered. Heuristic searches were conducted using 100 random addition sequences, and multiple states were treated as variable (ambiguous data were distinguished from polymorphic data). Characters were then reweighted using the rescaled consistency index, and a new heuristic search was performed. This process was repeated to determine if topology would continue to change with successive reweighting steps. Although there was minor variation in the number of steps following each reweighting/search iteration, tree topology never varied from the topology determined by the initial reweighting/search step. In all analyses the combined notauli character (#31) was used rather than the separate notaular characters (#32-34) to avoid overweighting of notauli. Two permutations of the data set were tested. First, *Bohpa* (Ceinae) was both included and excluded in analyses. Second, a data set was tested in which all bristle positional characters were removed (#22-30). The reasoning for these permutations is discussed in the previous section. Character state evolution was traced using MacClade (Maddison and Maddison 1992), and all indices mentioned were calculated from the analysis excluding *Bohpa* but including bristles unless otherwise noted.

Phylogenetic Results

The parsimony analysis excluding *Bohpa* but including bristle positional characters resulted in 472 trees (310 steps, not shown). After the characters were reweighted, the heuristic search resulted in 15 trees (strict consensus shown in Figure 1).

The parsimony analysis excluding *Bohpa* and bristle positional characters resulted in 437 trees (267 steps, not shown). After the characters were reweighted, the heuristic search resulted in 2773 trees (strict consensus shown in Figure 2). The parsimony analysis including *Bohpa* and bristle positional characters resulted in 118 trees (320 steps, not shown). After the characters were reweighted, the heuristic search resulted in 135 trees (strict consensus shown in Figure 3). The parsimony analysis including *Bohpa* but excluding bristles resulted in 1461 trees (276 steps, not shown). After the characters were reweighted, the heuristic search resulted in 120 trees (strict consensus shown in Figure 4).

Diparinae excluding *Liepara* Boucek, Eunotinae, and Coelocybinae were recovered as monophyletic in all analyses. In no analyses was *Liepara* recovered within Diparinae. *Liepara* appeared as sister-group to Diparinae when *Bohpa* was excluded. Ceinae was recovered as monophyletic in analyses excluding *Bohpa*, but paraphyletic as ((*Spalangiopelta* + *Cea*) + *Bohpa*) + Diparinae in analyses including the taxon. *Bohpa* was recovered as sister-group to Diparinae in analyses in which it was included. In three of the analyses, *Australolaelaps* + (*Neapterolelaps*, *Archaeolelaps*) represented the basal divergence within Diparinae, and in the fourth analysis only *Netomocera* was basal to it. In the analysis excluding *Bohpa* and including bristle positional characters, *Lelaps* was recovered as monophyletic. In the remainder of the analyses it was paraphyletic. *Dipara* was recovered as a paraphyletic grade in the analysis excluding *Bohpa* and including bristle positional characters, and in the remainder of the analyses was recovered as paraphyletic only with respect to *Pondia*. In all analyses *Boeria*, *Cerodipara*, and *Dozodipara* formed a paraphyletic grade at the base of the remaining diparines.

Bristle characters did not appear to uniformly impact tree construction between analyses both including and excluding *Bohpa*. Character state reconstructions for the bristle positional characters were examine using MacClade (Maddison and Maddison 1992), and different characters supported different clades. It is therefore unlikely that bristle positional characters are overwhelming other signal in the analyses, which suggests that bristles pairs in different positions are evolving independently. Second, when bristle positional characters were included, the only area of the tree where there was a transformation requiring a large number of steps was in the paraphyletic grade of *Boeria* and *Cerodipara*. In analyses where bristles were excluded, *Cerodipara* and *Boeria* were sister-taxa. However, this possible impact appears minor in comparison to the additional information provided by the bristle positional characters. Therefore, the analysis utilizing bristle positional characters was preferred.

The inclusion or exclusion of *Bohpa* had a dramatic impact on tree construction. When *Bohpa* was included it was sister-taxon to Diparinae, and this potential relationship is discussed below in the *Sister-Group Relationships* section. Additionally, the inclusion of *Bohpa* heavily impacted the internal phylogeny of Diparinae, most likely affecting the reweighting of characters important to the phylogeny of the derived diparines, because it had very little impact on which character states were ancestral for Diparinae. As *Bohpa* is flightless and appears highly modified for that role, it shares many characters with the more derived wingless diparines (e.g., a reduced metanotum), likely due to convergent evolution (in no analysis was *Bohpa* sister-group to the more derived diparines). This caused many characters which appear to be of high phylogenetic utility in the other

analyses to be strongly down-weighted in the reweighting step, as many characters became more homoplastic with *Bohpa*'s inclusion (e.g., the inclusion of *Bohpa* in the analysis drops the RCI of the metanotum character (#44) from 0.63 to 0.44). For the aforementioned reasons the tree excluding *Bohpa*was preferred with regard to the internal phylogeny of Diparinae, although *Bohpa* may represent the sister-group to Diparinae.

Evaluation of Traditional Characters

Although most diparines are easily recognized by chalcidologists, there has been no morphological evidence given to support their monophyly. They have traditionally been defined by various subsets of seven characters, although the phylogenetic value of these characters has not previously been examined. Additionally, these characters have only been used diagnostically in regional revisions, so their utility on a world level has also been unknown. The distribution of these characters throughout Diparinae and Pteromalidae is discussed below, and the phylogeny is used to evaluate their diagnostic utility.

1) Strong, dark bristles on the vertex and dorsal surface of the mesosoma (character #21). Although bristles are considered a trademark character for Diparinae, they are absent in many genera (e.g., *Neapterolelaps*, *Myrmicolelaps*) and their presence and thickness is variable in others (e.g., *Dipara*). Additionally, similar mesosomal bristles are present in many other pteromalids, including some eunotines, coelocybines, and species of *Spalangiopelta* (Ceinae). Only the configuration of the vertex bristles appears to be unique among the diparines. In Diparinae, the vertex bristles are arranged along the

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occipital margin, ocellar triangle, and along the dorso-frontal margins of the eyes (Fig.

18). In other pteromalids with vertex bristles, the bristles are often uniformly distributed

across the entire vertex (e.g., *Liepara*, *Lelapsomorpha* (Coelocybinae), *Spalangiopelta*

(Ceinae)). Based on the phylogeny, bristle presence/absence appear to be extremely

homoplastic (RCI = 0.12) within Diparinae and more broadly Pteromalidae, and provides

little phylogenetic or diagnostic utility.

2) Transverse striations on the posterior margin of the metacoxa (character #56).

Striations are present on most diparines, although they are absent in *Pseudoceraphron*

and *Nosodipara*, and their strength can vary dramatically within genera. The presence of

this character outside Diparinae is difficult to determine, as many pteromalids have some

sculpture on the posterior surface of the metacoxa, which is often difficult to judge

whether or not it is transversely striate. This character has limited phylogenetic and

diagnostic utility because of its sporadic loss within Diparinae (RCI = 0.19) and coding

difficulties outside of the diparines. However, this character does support a close

relationship between Diparinae + *Liepara*, with the character either evolving at the base

of (Diparinae + *Liepara*) + Eunotinae and being subsequently lost in *Moranila*, or being

independently derived in both Diparinae + *Liepara* and *Eunotus*.

3) High insertion of the metacoxa. Many diparines have their metacoxal insertion

significantly higher than their mesocoxal insertion. However, this character shows

continuous variation throughout Diparinae, and both coxae are inserted on the same level

in some genera (e.g., *Pseudipara*), making metacoxal striations difficult to use as a

diagnostic feature. This character was not coded for the phylogenetic analysis, because it could not be divided into discrete states.

4) Expanded first gastral tergite (GT1) covering at least a third of the metasoma (character #66). This character is present in all diparines except *Pyramidophoriella*, although it is also distributed throughout many pteromalid subfamilies (e.g., Eunotinae, some Miscogasterinae). As with the metacoxal striations, this distribution limits the character's diagnostic value. The ancestral condition within the Diparinae is an expanded GT1 (RCI = 0.38). An expanded GT1 appears to be sympleisiomorphic for Diparinae if *Liepara* is the sister-group, as it appears in the phylogeny to be synapomorphic for (Diparinae + *Liepara*) + Eunotinae. However, when *Bohpa* is sister-group to Diparinae, an expanded GT1 is synapomorphic for Diparinae. The expansion of GT1 may prove to have value in higher phylogenetic studies of Pteromalidae.

5) Antennae with one anellus, seven additional funicular segments, and three club segments (characters #15, 16, 74). This feature is broken up into three characters in the phylogenetic analysis: number of anelli in the female (#15), number of anelli in the male (#74), and number of flagellar segments (#16). These characters have little value for diagnosing diparines, as many diparine females have more than one anellus (e.g., *Nosodipara*, *Pseudoceraphron*), and many other pteromalid groups have similar antennal formulas (e.g., some Cleonyminae). The number of anelli in diparines appears to correlate with body size, as the most diminutive genera (e.g., *Pseudoceraphron*) have the most anelli, and in *Dipara* an increase in anellar number appears to correlate with a

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decrease in body size. Although these characters have limited diagnostic value, they do provide useful phylogenetic information and all have high consistency indices (#15: RCI=0.75; #74: RCI=1.00; #16: RCI=1.00). Presence of a single anellus is pleisiomorphic for the Diparinae when *Liepara* is sister-taxon and synapomorphic when *Bohpa* is sister-taxon. An increase in anellar number is synapomorphic for the *Nosodipara* + *Pseudoceraphron* clade, and a second increase is synapomorphic for *Pseudoceraphron*. The number of anelli in both males and females support a sister-group relationship of Ceinae + Coelocybinae rather than Ceinae + Diparinae. A reduced number of flagellar segments is synapomorphic for Eunotinae.

6) Female often wingless. This character is extremely plastic within Diparinae at the genus, species, and intraspecies level, and was therefore not coded in the analysis. For example, many genera contain both macropterous and apterous species (e.g., *Dipara*, *Lelaps*, *Parurios*), and Boucek (1988) noted a single species of Australian *Dipara* which had females showing the full range of macroptery, brachyptery, and aptery. Other characters included in the analysis provide a more accurate and less variable measure of 'potential' wing size. For example, the posterior notal wing process (#39) is always present and fully expanded in genera which have both macropterous and apterous species, while it is often reduced or absent in genera which have only wingless species. The diagnostic utility of aptery is limited; many wingless female pteromalids are diparines, but many female diparines are not wingless.

7) Presence of long cercal setae (character #69). This character is present throughout Diparinae and *Liepara*, and is the only synapomorphy for the combined group (RCI=0.38). The reconstruction of long cercal setae is ambiguous when *Bohpa* is sister-taxon to Diparinae.

Monophyly of Diparinae

While monophyly of Diparinae is supported in all analyses, the synapomorphies which unite the clade differ whether *Liepara* or *Bohpa* is considered the sister-taxon. Only a single synapomorphy unites Diparinae in both analyses: the presence of a cercal brush. When *Liepara* is considered sister-taxon to Diparinae, diparine monophyly is supported by five additional synapomorphies: lack of a smooth, convex dorsellum, presence of sexual dimorphism, presence of an occipital carina, presence of admarginal setae, and a long marginal vein. When *Bohpa* is considered sister-taxon to Diparinae, diparine monophyly is supported by three additional synapomorphies: an expanded GT1, transverse striations of the posterior margin of the metacoxa, and a single anellus in the female. Diparinae is diagnosable by a combination of two of these features: lack of a smooth, convex dorsellum and presence of a cercal brush. Those characters which have not already been analyzed are discussed below.

1) Presence of a cercal brush (character #70). All diparines have a cercal brush (which is defined in the Methods section). The size and density of the brush varies throughout the Diparinae, but it is always present (Figs. 13, 17, 34, 35, 41). The cercal brush is synapomorphic for Diparinae in all analyses (RCI=1.00). In a broad survey of

Pteromalidae, the cercal brush was only noted in two other taxa. First, *Spalangia* (Spalangiinae) possesses a similar brush. The spalangiines appear to be unrelated to the diparines, as they have little morphological similarity, and molecular evidence also suggests a lack of close relations (Desjardins et al, in press). The presence of this character in both taxa could represent convergent evolution, as both taxa inhabit similar environments. The only other genus in Spalangiinae, *Playaspalangia*, was not examined for this character. However, *Playaspalangia* is a rare genus known only from Mexico and Sri Lanka, which parasitizes Diptera under rotting algae (Yoshimoto 1976), and may be a highly derived species of *Spalangia*. Additionally, a sparse cercal brush was found on the holotype of *Spalangiopelta ferrierei*, although it appeared absent on the two additional female specimens of the species. To assess the state of this character throughout *Spalangiopelta*, multiple specimens of 3 additional *Spalangiopelta* species were examined (*S. canadensis*, *S. ciliata*, and *S. felonia*). None of these species showed any evidence of a cercal brush, so the character is coded as absent in the genus, with the sparse brush in *S. ferrierei* being considered an aberrant condition.

2) Absence of a broad, convex dorsellum (character #42). All diparines lack a broad, convex, dorsellum (Figs. 10, 19, 29, 38, 48, 50, 51, 55) (RCI=1.00). In some diparines the metanotum is absent entirely, so the theoretical presence of a dorsellum cannot be ruled out in those taxa. However, the most primitive diparines do possess a metanotum which is not reduced, and lack a dorsellum, so it is unlikely that the dorsellum is "hypothetically regained" in taxa lacking a metanotum. A reduced, smooth metanotum without a convex dorsellum has been noted in other pteromalids, particularly *Bohpa* and

an undescribed, apterous cleonymine from Madagascar. Additionally, this state is

present in the apterous encyrtid *Tetracyclos boreios* (redescribed in detail by Gibson and

Yoshimoto 1981). This reduction may be an adaptation for increased mesosomal

mobility in apterous chalcidoids, and therefore may have been independently derived in

Bohpa. However, the ancestral state in Diparinae is macroptery, so aptery cannot fully

explain the loss of the dorsellum within Diparinae. This feature is synapomorphic for

Diparinae when *Liepara* is its sister-taxon and Diparinae + *Bohpa* when *Bohpa* is its

sister-taxon. Moranilines (Eunotinae) also lack a broad, convex, dorsellum, and instead

have a cup-shaped projection issuing from the medial portion of the metanotum.

However, this configuration is different from the undifferentiated metanotum in diparines

and is coded as a separate state.

3) Sexually dimorphic (character #71). Most diparines with known males are sexually

dimorphic, although this trait was lost once within the group (CI=0.28). When *Liepara* is

considered sister-taxon to Diparinae, sexual dimorphism evolves twice independently,

once in Diparinae and once in *Spalangiopelta*. Alternatively, in analyses including

Bohpa, sexual dimorphism evolves at the base of the Ceinae and is subsequently lost in

Cea or evolves twice independently in Diparinae + *Bohpa* and *Spalangiopelta*. Despite

the phylogenetic value of sexual dimorphism, it provides little diagnostic utility. Most

often only single specimens are available for identification purposes, and even when

multiple specimens are present, it is difficult to identify them as con-generic or -specific.

4) Presence of an occipital carina (character #6). The presence of an occipital carina appears to be synapomorphic for Diparinae when Liepara is its sister-group (RCI=0.13), although in analyses including *Bohpa*, it evolves at the base of the Ceinae and is subsequently lost in *Cea* or evolves twice independently in Diparinae + *Bohpa* and *Spalangiopelta*. Its low consistency index and sporadic distribution throughout Pteromalidae make the occipital carina's phylogenetic utility difficult to judge. A selection of outgroups which have occipital carinae would likely have given different results. The presence of an occipital carina has no diagnostic value for Diparinae, as the trait is transformed multiple times within the group.

5) Admarginal setae (character #59) and 6) Long marginal vein (character #60). These character are discussed below in the *Sister-Group Relationships:* Bohpa *Darling* section.

Sister-Group Relationships: Liepara *Boucek*

In his revision of the Australasian Chalcidoidea, Boucek (1988) synonomized the existing tribes of Diparinae and erected a new tribe within the subfamily, Lieparini, for the newly described genus *Liepara*. Although Boucek made no specific statement that *Liepara* was sister-group to the remainder of the Diparinae, his tribal classification suggests this relationship. Boucek united *Liepara* with the Diparinae based on five characters: 1) antennal formula 11173, with a clearly three-segmented symmetrical clava, 2) GT1 distinctly enlarged, 3) hind coxa inserted fairly high, 4) hind coxa with distinct transverse striations, and 5) typical diparine-like pattern of bristles. As discussed above,

many of these characters have limited phylogenetic value, due to their sporadic presence throughout Pteromalidae (1, 2, 5) or coding difficulties (3, 4), and none of these characters appear to be synapomorphic for Diparinae + *Liepara* or place *Liepara* within Diparinae (with the possible exception of 4, discussed below). The pattern of vertex bristles is particularly interesting, because the interpretation of *Liepara*'s vertex bristles here differs from that of Boucek (1988).   As already noted, the vertex bristles of diparines are arranged along the occipital margin, ocellar triangle, and along the dorso-frontal margins of the eyes. The vertex bristles on *Liepara* appear to uniformly cover the vertex, and more closely resemble the bristles of *Lelapsomorpha* and *Spalangiopelta* than those of Diparinae. While *Lelapsomorpha* and *Spalangiopelta* appear to have a much greater number of bristles than *Liepara*, they also have a much smaller scrobe and larger vertex, providing more positionally homologous space for the placement of bristles.

Liepara does not appear to belong to Diparinae and in particular lacks the highly consistent cercal brush and a medially undifferentiated metanotum. *Liepara* appears as the sister-group to the remainder of Diparinae in phylogenetic analyses excluding *Bohpa*, although the only synapomorphy uniting this clade is long cercal setae (#69). The presence of metacoxal striations (#56) also supports this relationship in one of two most parsimonious reconstructions (the other reconstruction is ambiguous). Additionally, this sister-group relationship is supported by biogeography. The most basal lineage of diparines, the Neapterolelapini, has an Australasian distribution, as does *Liepara*. *Netomocera*, another primitive diparine, is also present in this region. Ceinae, on the other hand, which will be discussed below as another potential sister-group to Diparinae, is one of the few pteromalid subfamilies absent from the Australasian region.

Even if *Liepara* is sister-group to Diparinae as presented here, maintaining *Liepara* within Diparinae would greatly weaken the definition of the latter group. Two qualitative diagnostic features would be eliminated and replaced with a single character which is much more difficult to diagnose, as the length of the cercal setae is more quantitative than qualitative. Additionally, the support for *Liepara* as sister-group to Diparinae is not strong, as *Bohpa* is recovered as sister-group to Diparinae when included in the analysis. The taxonomic effects of removing *Liepara* from Diparinae and *Liepara*'s placement within Pteromalidae are further discussed in the genus' treatment in the generic revision.

Sister-Group Relationships: Bohpa *Darling*

Ceinae is a cosmopolitan (although absent from the Australasian region) pteromalid subfamily including three genera: *Bohpa*, *Cea*, and *Spalangiopelta*. In the phylogenetic analysis excluding *Bohpa,* Ceinae was resolved as monophyletic based on five synapomorphies, only the first of which is not homoplastic: presence of claval peg-like sensillae, first funicular segment subequal in length to pedicel, presence of admarginal setae, marginal vein long, and toruli within 1 torulus diameter from the oral fossa. In these analyses, Ceinae was placed as sister-group to Coelocybinae based on three synapomorphies: female with three anelli, male with three anelli, and GT1 not expanded. The number of anelli may not be independent between non-sexually dimorphic taxa, although *Spalangiopelta* shows both sexual dimorphism and three male anelli, while all diparines, whether sexually dimorphic or not, have only one anellus in the male.

When *Bohpa* is included, however, Ceinae appears paraphyletic as ((*Spalangiopelta* + *Cea*) + *Bohpa*) + Diparinae. The entire clade is supported by two synapomorphies: the presence of admarginal setae and a long marginal vein. The reconstruction of sexual dimorphism is ambiguous in part because the male of *Bohpa* is unknown; in one reconstruction it is gained independently in *Spalangiopelta* and *Bopha* + Diparinae, in the second it is gained at the base of the entire clade and subsequently lost in *Cea*. Regardless, both reconstructions support a close relationship between Diparinae and Ceinae. The clade of *Bohpa* + Diparinae is supported by the loss of the dorsellum, and *Spalangiopelta* + *Cea* is supported by claval peg-like sensillae. Darling (1991a) discusses six characters traditionally used to define Ceinae, and their relevance to a mono- and paraphyletic Ceinae are discussed here.

1) Complete notauli. This state appears pleisiomorphic for both a mono- and paraphyletic Ceinae, as all taxa included in the analysis except for the coelocybines and *Pyramidophoriella* have complete notauli.

2) Propodeal spiracles positioned halfway along antero-posterior axis of propodeum. Darling mentions the presence of this character in some Colotrechninae. Whether this character state is present in some diparines depends on whether or not the nucha is included in the propodeal measurement. Some diparines with a long nucha, such as *Myrmicolelaps*, have a fairly posteriorly placed spiracle. If the propodeum is measured without the nucha, the spiracle is positioned medially. However, if the propodeum is measured with the nucha, the propodeal spiracle is positioned anteriorly.

Regardless, this state would be derived within the diparines, as all basal diparines have anteriorly positioned spiracles. Although not coded in the analysis, this would support a monophyletic Ceinae.

3) Toruli situated within 1 torulus diameter from oral fossa. This state is only present in the derived diparine genera *Boeria* and *Cerodipara*. Darling mentions the lower positioning of the toruli occurs in some neodiparines, eunotines, cleonymines (Graham 1969), and colotrechnines (Boucek 1988). Within this phylogenetic analysis, torular position supports a monophyletic Ceinae when *Bohpa* is excluded, and is gained at the base of ((*Spalangiopelta* + *Cea*) + *Bohpa*) + Diparinae and subsequently lost in Diparinae when *Bohpa* is included.

4) Antennal formula 11353. Darling (1991a) notes the presence of three anelli in some Pteromalinae, Miscogasterinae, and Pireninae. The presence of three anelli in both sexes is also found in Coelocybinae and when *Bohpa* is excluded is synapomorphic for Coelocybinae + Ceinae. However, when *Bohpa* is included, this feature is independently derived in Coelocybinae and ((*Spalangiopelta* + *Cea*) + *Bohpa*) + Diparinae, and subsequently lost in Diparinae.

5) Marginal vein long. Darling does not discuss the distribution of this character throughout Pteromalidae, but this feature is synapomorphic for ((*Spalangiopelta* + *Cea*) + *Bohpa*) + Diparinae when *Bohpa* is included. When *Bohpa* is excluded, a long marginal vein is independently derived in Diparinae and Ceinae.

6) Mandibles bidentate. As with the marginal vein, Darling does not discuss the distribution of this character. This character was not treated in the phylogenetic analysis due to the difficulty of coding many diparine genera known from only a few specimens whose mandibles could not be observed.

Prior to the description of *Bohpa*, Darling (1991a) hypothesized that ceines weremonophyletic based on two putative synapomorphies, the first of which is a reduced number of papilliform sensilla. He hypothesized that Diparinae + Ceinae is defined by papilliform sensilla, and further that Ceinae is defined by a reduced number of those sensilla (alternatively, in an equally parsimonious explanation, Diparinae could be defined by an increased number of papilliform sensillae). As defined by Darling (1991a), papilliform sensillae are socketed, lobate setae that appear in pairs on the apical margin of the funicular segments in ceines. These structures were previously unknown in the Chalcidoidea. Some eulophids have more simple, unsocketed, randomly placed structures termed "multiporous pegs", but Darling stated that the two are likely not homologous. Darling sampled representatives from 15 pteromalid subfamilies, and papilliform sensillae were found only on *Lelaps*, a member of Diparinae. Although such a complex character showed potential as a strong synapomorphy uniting ceines and diparines, Darling only investigated a single member of Diparinae. Unfortunately, this character could not be utilized in the phylogenetic analysis, as specimens of many diparine genera were unavailable for slide mounting or scanning electron microscopy. However, a variety of diparines were examined for this feature.

The antennae of males of four available diparine genera (*Lelaps*, *Netomocera*, *Parurios*, and *Australolelaps*) were slide mounted in Hoyer's (results not shown). The slide of *Lelaps* was prepared as a positive control, in order the establish the position and visibility of the sensilla. Papilliform sensillae were found in all four genera (including the primitive *Australolaelaps*), suggesting that the presence of sensilla is the ancestral state for Diparinae. Antennal SEMs of the female of *Pseudoceraphron* (Diparinae) reveal a lack of the papilliform sensilla. This may be an artifact of the placement of papilliform sensilla, which in females are most often located beneath the dorsally extended apex of the multiporous plate sensilla. The female of *Pseudoceraphron* has a largely reduced funicle (7-8 segments are anelliform). Anelliform segments by definition lack multiporous plate sensilla, and therefore the majority of funicular segments in *Pseudoceraphron* lack a positionally homologous location for the placement of papilliform sensilla. As the male of *Pseudoceraphron* is not known for certain, it could not be examined for these sensilla. Additionally, close investigation of antennal SEMs in Gibson's revision of Eupelminae (1995) have revealed papilliform sensilla on a large number of eupelmids (e.g. *Zaischnopsis*, Fig. 354; *Reikosiella*, Figs. 367-368). Although this character may still prove useful in the phylogenetics of pteromalid subfamilies, its distribution must be more carefully examined.

Darling termed his second ceine synapomorphy "claval peg-like sensillae." However, later that year he published the description of *Bohpa* (1991b), in which he stated that *Bohpa* has neither the papilliform nor claval peg-like sensillae. Phylogenetic analyses in which *Bohpa* was included would suggest papilliform sensillae were lost in *Bohpa*, and claval peg-like sensillae are synapomorphic for *Spalangiopelta + Cea*. The

exceptionally small size of *Bohpa* may have resulted in the reduction or loss of many features, including antennal ones. It is difficult to speculate on character evolution within Ceinae, however, as in a 3 taxon clade a gain and a loss are equally as parsimonious as two independent gains of a character state. Additionally, and outgroups in this analysis were chosen to reflect possible diparine relationships rather than ceine ones.

In addition to the presence of papilliform sensillae, Darling (1991a) proposed the presence of admarginal setae on the inner leading margin of the forewing membrane in both ceines and diparines. The presence of these setae does appear synapomorphic for ((*Spalangiopelta* + *Cea*) + *Bohpa*) + Diparinae in this phylogenetic analysis. Darling suggested that these setae might hold the hindwing tight against the body during movement in confined spaces. During the course of this study, many diparine specimens were observed in which the setae appear to hold the hind wing in place while they are folded against the body. However, it should be noted that since both diparines and ceines search for hosts in leaf litter, this character could be a result of convergent evolution.

Inclusion of additional characters could help elucidate the relationship between Ceinae and Diparinae. The addition of a propodeal spiracle position would lend support to Ceine monophyly, while a papilliform sensillae character would lower support for a *Bohpa* + Diparinae relationship. However, knowledge of the male of *Bohpa* could potentially provide the strong support for a *Bohpa* + Diparinae relationship. If *Bohpa* is sexually dimorphic, this would support a close relationship between Ceinae and Diparinae, as the genus is likely sexually dimorphic. Also, if the male of *Bohpa* is winged and has admarginal setae and a long marginal vein, this could be the decisive

evidence indicating *Bohpa* as the sister-taxon to Diparinae rather than *Liepara*. For now,

however, the sister-group to Diparinae will have to remain in question.

Systematics of the world genera of Diparinae

Diparinae Thomson

Diagnosis: Diparinae can be diagnosed by a combination of two features: presence of a cercal brush (Figs. 13, 17, 34, 35, 41) and absence of a smooth, convex dorsellum (Figs. 10, 19, 29, 38, 48, 50, 51, 52). Additionally, the vast majority of diparines have a GT1 expanded to cover at least ½ the metasoma (Figs. 12, 34) and transverse striations on the posterior margin of the metacoxa (Figs. 21, 28, 32, 54). Females are often apterous or brachypterous.

Taxonomic History: Thomson (1876, 1878) first described the group as "subtribus Diparides" within Pteromalidae. Ashmead (1904) treated Diparinae as a subfamily of Pteromalidae and Lelapinae as a subfamily of Miscogasteridae based on the median clypeal tooth found in *Lelaps*. Peck (1951) proposed the tribe Diparini and placed it within Sphegigasterinae. Boucek (1954) synonomized the two subfamilies of Ashmead, without referencing Peck. Delucchi (1962) kept Boucek's subfamily status, but returned Diparini to tribal status and created a new tribe, Lelapini. He separated these tribes based on differences of the clypeus, pronotum, antennae, and bristles, although he did not qualify these differences. Hedqvist (1969) retained the two as separate tribes without referencing Delucchi's identical tribal classification (as noted in Heydon and Boucek (1992)). Hedqvist included *Lelaps* Walker and the Hawaiian genera (*Calolelaps* Timberlake, *Mesolelaps* Ashmead, *Neolelaps* Ashmead, and *Stictolelaps* Timberlake) in Lelapini, while he placed the remaining genera in Diparini. Heydon and Boucek (1992)

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also noted that it appeared that Hedqvist had replaced the clypeal tooth character of Ashmead with brachyptery versus macroptery, as Hedqvist considered *Spalangiolaelaps* Girault (which has wingless females and a median clypeal tooth) to be part of Diparini. Hedqvist (1971) added a third tribe, Netomocerini, which contained only the genus *Netomocera* Boucek. Although he defined the tribe, none of the characters he listed were unique to *Netomocera* within Diparinae. Yoshimoto (1977) followed the classification of Hedqvist (1969, 1971), apparently also unaware of Delucchi's (1962) proposal. Boucek (1988) proposed that the three tribes were unnecessary, and Lelapini and Netomocerini should be synonomized within Diparini. He erected a second tribe, Lieparini, for the aberrant genus *Liepara* Boucek. Heydon and Boucek (1992) followed Boucek's (1988) tribal classification based on the presence of intermediates between the three tribes Diparini, Lelapini, and Netomocerini.

Discussion: The monophyly of Diparinae has been previously discussed in the *Monophyly of Diparinae* section. Therefore the tribe Lieparini is also removed from Diparinae and becomes unplaced within the Pteromalidae.

Biology: Although the first diparine was described over two hundred years ago, virtually nothing has been known about their biology. The first host was reported by Boucek (1988), in which an undescribed Indian species of *Parurios* was reared from a curculionid (Coleoptera) feeding on the roots of *Cyperus*. Since most female diparines are collected in forest leaf litter, and the only published host record is a curculionid, it has often been extrapolated that the entire subfamily parasitizes soil-inhabiting Coleoptera

(e.g., Boucek 1988). In accordance with this hypothesis, Texas A&M entomologists reared *Lelaps sp.* from boll weevil relatives in southern Mexico (J. Woolley, pers. comm.). Weevil parasitism certainly does not apply to all diparines, however, as an undescribed species of the African *Myrmicolelaps* was reared from mantid egg cases (Prinsloo pers. comm.), and an additional undescribed species was reared from a tsetse fly puparium (Glossinidae: *Glossina*). These data suggest that "typical" diparines may primarily parasitize beetles (and more specifically weevils), as has been suggested in the literature for some time. Second, that some morphologically bizarre diparines also possess deviant biologies, and that parasitism of beetles certainly does not extend throughout the subfamily.

Key to the genera of Diparinae

1.   Female   2

      Male   15

2. (1) Metacoxa with thick vertical brush of white setae on posterior margin (Fig. 39);

        anterior surface of GT1 lateral to petiole with thick tufts of white setae (Figs. 37,

        50, 51); longest metatibial spur at least 2X width of metatibia at point of insertion

        (Fig. 40)   *Neapterolelaps* Girault

        Without thick patches of setae on metacoxae (Figs. 21, 28, 46) or GT1 (Fig.);

        longest metatibial spur at most 1.5X width of metatibia at point of insertion (Fig.

        32, 33) (questionably 1.5-2X in *Pseudoceraphron regieri*)

                                                                3

3. (2)   Mesepisternum with tranverse, cylindrical, black depression (Fig. 46); apical

clypeal margin concave (Fig. 45); antenna with at least 4 anelli (Fig. 42); eye

normal, with over 50 facets (Fig. 44); Australasian distribution

4

Mesepisternum without transverse, cylindrical, black depression (Fig. 20, 28);

apical clypeal margin not concave (may be convex, bilobed, (Fig. 27) or with

median tooth (Fig. 16)); antenna with 2 or fewer anelli (or rarely, if appearing to

have 3-4 anelli, then eye reduced with less than 30 facets); Cosmopolitan

distribution   5

4. (3)   Antenna with 7-8 anelli; posterior margin of gena carinate; posterior surface of

metacoxa concave (Fig. 49); scutellum flat (Figs. 47, 48)

Pseudoceraphron Dodd

Antenna with 4-5 anelli; posterior margin of gena rounded; posterior surface of

metacoxa convex (Fig. 21); scutellum convex (Fig. 10)

Nosodipara Boucek

5. (3)   Petiole at least 2X as long as wide, and either bent sharply ventrally at 90° angle

or strongly constricted antero-ventrally (Figs. 12, 34); clava 1- or 2-segmented

(either all or 2nd and 3rd claval segments fused (Fig. 6))

6

Petiole usually less than 1.5X as long as wide, always straight, and never

constricted antero-ventrally (or petiole not visible (Fig. 20)); clava distinctly 3-

segmented (Fig. 15)   8

6. (5) Nucha with 2 dorso-lateral horn-like projections; petiole bent sharply ventrally at 90°; propodeal foramen circular, open only in 1 plane (Fig. 49); Afrotropical distribution   *Conodipara* Hedqvist

Nucha without dorso-lateral horn-like projections; petiole straight and strongly constricted antero-ventrally (Figs. 12, 34); propodeal foramen hinge-like, open posteriorly and ventrally (Fig. 31); Cosmopolitan distribution

7

7. (6) Toruli on shelf (upper and lower face separated by carinate angle of 90° (Fig. 8)); axillary wing sclerite not visible   *Conophorisca* Hedqvist

Toruli not on shelf (upper and lower face separated by carinate or rounded angle of less than 50°); axillary wing sclerite expanded and visible (Fig. 30)

Myrmicolelaps Hedqvist

8. (5) Prepectus small, not reaching tegula (lateral scutal margin either touches mesopleuron or is separated from it by an anteriorly extended tegula (Fig. 54)); Afrotropical distribution   9

Prepectus large, reaching tegula (lateral scutal margin does not touch mesopleuron (Fig. 20)); Cosmopolitan distribution   12

9. (8) Toruli on shelf (upper and lower face separated by carinate angle of 90° (Fig. 8)); 1 metatibial spur; Madagascar   *Dozodipara* Desjardins, new genus

Toruli not on shelf (upper and lower face separated by carinate or rounded angle of less than 50°); 2 metatibial spurs; Continental Africa

10

10. (9) Notauli completely absent; propodeum with 2 large dorso-lateral horns, with propodeal spiracles situated on the lateral surface of horns (Fig. 55)

Pyramidophoriella Hedqvist

Notauli present; propodeum without horns 11

11. (10) With many pairs of strong, dark bristles on vertex and dorsal surface of mesosoma; propodeum gently sloping, longer than high

Boeria Hedqvist

With only a single pair of strong, dark bristles on postero-lateral margin of frenum; propodeum steeply sloping, higher than long

Cerodipara Desjardins, new genus

12. (8) Clava asymmetrical *Netomocera* Boucek

Clava symmetrical 16

13. (12) Three pairs of scutellar bristles; anellus longer than broad; Neotropical distribution *Chimaerolelaps* Desjardins, new genus

At most 2 pairs of scutellar bristles; anellus broader than long; Cosmopolitan distribution 14

14. (13) Clypeus without median tooth (Fig. 27, 44); F1 subequal in length to F2

Dipara Walker

Clypeus with median tooth (Fig. 16); F1 at least 1.5X as long as F2

Lelaps Walker

15. (1) Metacoxa with thick vertical brush of white setae on hind margin; anterior surface

of GT1 lateral to petiole with thick tufts of white setae; longest metatibial spur at

least 2X width of metatibia at point of insertion   *Neapterolelaps* Girault

Metacoxa without thick patches of setae on either the metacoxa or GT1; longest

metatibial spur at most 1.5X width of metatibia at point of insertion

16

16. (15) Petiole either bent sharply ventrally at 90° angle or straight and strongly

constricted antero-ventrally (Figs. 12, 34); nucha at least as long than wide;

acropleuron broadly expanded (Fig. 28); apterous; Afrotropical distribution

17

Petiole neither L-shaped nor strongly constricted antero-ventrally, may not be

visible in lateral view; nucha wider than long; acropleuron normal, not broadly

expanded (Fig. 20); usually macropterous (but may be brachypterous or

apterous); Cosmopolitan distribution   19

17. (16)Nucha with 2 dorso-lateral projections; petiole L-shaped; propodeal foramen

circular, open only in 1 plane   *Conodipara* Hedqvist

Nucha without dorso-lateral projections; petiole straight and strongly constricted

antero-ventrally (Figs. 12, 34); propodeal foramen hinge-like, open posteriorly

and ventrally (Fig. 31)   18

18. (17)Toruli on shelf (upper and lower face separated by carinate angle of 90° (Fig. 8));

axillary wing sclerite not visible   *Conophorisca* Hedqvist

Toruli not on shelf (upper and lower face separated by carinate or rounded angle

of less than 50); axillary wing sclerite visible and expanded (Fig. 30)

Myrmicolelaps Hedqvist

19. (16)Petiole at most as broad as long   *Netomocera* Boucek

Petiole at least 2X longer than broad   20

20. (19)Clypeus with median tooth (Fig. 16); funicular segments cylindrical and at least

1.5X as long as wide   *Lelaps* Walker

Clypeus without median tooth (Fig. 27, 44); funicular segments either

pedunculate or less than 1.5X as long as wide   *Dipara* Walker

Boeria Hedqvist

Boeria Hedqvist 1969: 185. Type species: *Boeria saetosa* Hedqvist (orig. desig. and by

monotypy).

Diagnosis: *Boeria* is known only from females, and can be diagnosed by a combination

of features. First, the toruli are situated low on the face, approximately 2 torulus

diameters from the oral fossa. *Boeria* shares this character with *Cerodipara*, although the

toruli are situated at least 4 torulus diameters from the oral fossa in the remainder of the

diparines. Three features exist to distinguish *Boeria* from *Cerodipara*. First, *Boeria* has

many pairs of bristles present on the vertex and dorsal surface of the mesosoma, while *Cerodipara* has only a single pair of scutellar bristles on the lateral edges of the frenal line. Also, *Boeria* has a gently sloping propodeum which is longer than high (Figs. 56, 57), while *Cerodipara* has a steeply sloping propodeum which is higher than long (Fig. 58). Third, *Boeria* has parallel-sided inner eye margins, while *Cerodipara* is the only diparine to have ventrally diverging inner eye margins. *Boeria* is also the only diparine with a full complement of bristles and a broadly expanded acropleuron.

Discussion: Although the male of *Boeria* is unknown, given the genus' placement in the phylogeny it would be expected to be sexually dimorphic. However, the male is also unknown for closely related genera, including *Cerodipara* and *Pyramidophoriella*. Only 5 specimens are known to exist, and it is possible that males are not sexually dimorphic, but have just not been collected. It is difficult to speculate on what the males of *Boeria* would look like, but given the males of *Pondia*, and the proposed males of *Pseudoceraphron*, it would appear that *Boeria* males would have pedunculate flagellar segments with long, apically appressed setae.

Boeria is phylogenetically positioned in a basal grade with *Pondia*, *Cerodipara*, and *Dozodipara*, leading to the most derived diparines.   The clade of diparines inclusive of *Boeria* is defined by 2 synapomorphies: a broadly expanded acropleuron and strongly arched notauli which meet the posterior scutal margin at the scutoscutellar suture. *Boeria* is also one of the few taxa whose phylogenetic positioning may be adversely affected by the inclusion of bristle characters. In all analyses excluding the bristle positional characters, it is sister-taxon to *Cerodipara*. These two genera have a number of features

in common, particularly the lower positioning of the toruli, which is unique to these taxa among Diparinae. However, *Boeria*, which in analyses including bristle positional characters is positioned basal to *Cerodipara*, has a large complement of bristles, as does *Pondia*, which is positioned basal to *Boeria*. None of the taxa more derived than *Cerodipara* have any bristles. The inclusion of bristle positional characters causes a sister-group relationship between *Boeria* and *Cerodipara* to cost 4 additional steps, which may inaccurately outweigh otherwise strong synapomorphies.

Number of Species: 1 described.

Distribution: South Africa (Western Cape, Eastern Cape).

Hosts: Unknown.

Key to Species: None.

Species of *Boeria:*

saetosa   Hedqvist. AFROTROPICAL: South Africa.

> *Boeria saetosa* Hedqvist 1969: 185-186 (Fig. 8). Holotype female: S. Africa, Pondoland, Port St. John, Jan. 1924. coll. R. E. Turner. (BMNH, examined). 4 Paratype females: S. Africa, Pondoland, Port St. John, Dec. 1923 (1 female), 29.I-15.II.1924 (1 female), 1-17.III.1924 (1 female), and Cape Prov., Somerset East, 1-26.I.1921 (1 female). coll. R. E. Turner. (BMNH, examined).

Cerodipara Desjardins, New Genus

(Fig. 58)

Type Species: *Cerodipara sabensis* Desjardins, New Species

Diagnosis: *Cerodipara* is unique among the diparines in having ventrally diverging inner eye margins, vertical carinate ridge running from interantennal area to anterior clypeal margin, and only a single pair of bristles positioned on the posterior margin of the scutellum. In addition, the toruli of *Cerodipara* are positioned approximately 2 torulus diameters from the oral fossa. Only *Boeria* has similarly positioned toruli. Additional characters used to separate *Cerodipara* from *Boeria* are discussed in the *Boeria* diagnosis.

Description: Female. *Head:* Occipital margin rounded; occipital carina absent; upper face without strong, transversely carinate sculpture; eyes not posteriorly extended beyond occipital margin; inner eye margins ventrally diverging; eyes bare; scrobe present and scrobal channel parallel-sided; dorsal margin of scrobe rounded; toruli not on shelf, junction between upper and lower face rounded; toruli within 2 torulus diameters of ventral margin of face; antennae symmetrically clavate; antennal formula 11173; pedicel, first funicular segment, second funicular segment subequal in length; claval apex without thick tuft of micropilosity; apical clypeal margin symmetrically bilobed; clypeus with medial longitudinal carina; malar groove present; strong, dark bristles on vertex absent. *Mesosoma:* dorsum of mesosoma with single pair of strong, dark bristles on posterior

half of scutellum; pronotum short, collar-like; notauli strongly arched along entire length (appearing semi-circular) and meeting posterior scutal margin at scutoscutellar suture; lateral lobes of scutum similar in color to remainder of scutum; posterior scutal margin without setose groove; scutellum large, slightly convex, not descending posteriorly; axillae reduced and concave; posterior notal wing process present but truncate, rounded; frenum absent; metanotum present as narrow, sculptured band; propodeum at least 1.5X higher than long; propodeum without medial spine; plicae absent; suture between postspiracular area and metapleuron diagonal; propodeal foramen circular, open in one plane; mesepisternal depression absent; prepectus reduced, not reaching tegula; tegula normal, flap-like; subalare not visible; acropleuron large, convex, broadly expanded along dorsal length of mesopleuron; mesopleuron smooth posteriorly; metacoxa posteriorly convex, with transverse striations; metacoxa posteriorly without thick vertical brush of seta; 2 metatibial spurs, longer spur <1.5X width of tibia at point of insertion. *Metasoma:* Petiole cylindrical, without setae, broader than long; GT1 expanded, covering at least half of metasoma length; GT1 rounded lateral to petiole insertion; cercal setae elongate; cercal brush present. **Male:** Unknown.

Discussion: In the phylogenetic analysis, *Cerodipara* is positioned in a basal grade with *Pondia*, *Cerodipara*, and *Dozodipara*, leading to the most derived diparines. The clade inclusive of *Cerodipara* is defined by 3 synapomorphies: a symmetrically bilobed apical clypeal margin, loss of the anterior scutellar bristles, and loss of the frenum. The relationship between *Cerodipara* and *Boeria* is discussed in the latter taxon's generic

entry. As *Cerodipara* is known only from the female holotype specimen, it is difficult to speculate on the morphology of the male.

Etymology: *cero-*, meaning horn or crest, after both the genus' superficial resemblance to Cerocephalinae and the carinate ridge running between the toruli. *-dipara* to ally the genus with Diparinae.

Number of Species: 1 described (South Africa: Mpumalanga).

Distribution: South Africa

Hosts: Unknown.

Cerodipara sabensis Desjardins, New Species

(Fig. 58)

Type information: Holotype female, SAM: "South Africa, Eastern Transvaal, Sabi Sand Game Reserve, 24°46'S 31°22'E, 11 September 1994, J. Swart, Pitfall Trap, SLE."

Description: Female. 2.1 mm. *Color:* Brownish orange, with the following exceptions: scape off-white; pedicel medially light brown; F6-7+clava brown; coxae off-white; legs pale brownish yellow; ventral 1/2 of GT1 brown; tip of ovipositor sheath light brown. *Head:* Ovate in frontal view, about as wide as high; vertex rugulose, becoming areolate on upper and lower face; ratio of ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 2.2: 4.2: 2.4: 1; scrobe high, reaching to within half an ocellar diameter from midocellus; scrobal basin and walls transversely striate-reticulate;

interantennal carina strong, reaching about 0.5X height of scrobe; toruli separated by 1.1 torulus diameters; antennae clavate; scape height subequal to eye height; anellus about 4X broader than long; ratio of scape: pedicel: anellus: F1: F2: F3 about 52: 12: 1: 9: 9: 8; F4 and F5 slightly broader than long; clypeus well delimited. *Mesosoma:* Dorsally transversely striate-reticulate, becoming circularly striate-reticulate on scutellum; ratio of pronotum: scutum: scutellum: propodeum about 2.5: 1.9: 2.2: 1; mesosoma dorsally covered in fine, white setae; pronotum, scutum, and scutellum dimensions difficult to measure due to specimen orientation; marginal rim of scutellum smooth; metanotum narrow band with pits delimited by longitudinal striae; propodeum anteriorly with semicircular carina opening anteriorly and single longitudinal carina medially within semicircle; propodeal sculpture smooth within semicircle, rough with irregular longitudinal carinae anterior to semicircle, reticulate lateral to semicircle; nucha narrow and roughly sculptured; plicae absent; postspiracular sulcus smooth and bare; spiracle 1.5X own diameter from metanotum; callus bare, projecting posteriorly beyond postspiracular sulcus into upturned point; prepectus triangular, not in same plane as pronotum, abutting at about 135º angle; mesepimeron transversely striate dorsally and smooth ventrally; femoral depression deep, transversely striate dorsally, areolate ventrally, well defined anteriorly and posteriorly; metapleuron medially smooth, with narrow, finely pitted anterior margin and wide, deeply pitted posterior margin; pro- and mesocoxa with sparse white setae on disto-anterior margins; meso- and metatibia spinose; longer metatibial spur about 2.5X length of shorter, about 0.5X width of metatibia at point of spur insertion; metabasitarsus about 3X as long as wide, about 0.3X length of remaining tarsi; hind coxae distinctly transversely striate; wings apterous,

forewing preset only as membranous lump with single long, dark bristle, hindwing entirely absent. *Metasoma:* About 1.1X length of mesosoma; ratio of GT1: GT2-6:GT7:ovipostor sheaths about 4.6:1.3:1.3:1; GT1-4 and ovipositor sheath dorsally with sparse, white setae; GT4-7 and ovipositor sheath laterally with sparse white setae; ovipositor apico-dorsally obscured by sheath. **Male:** Unknown.

Etymology: Named for the Sabi Sand Game Reserve in which the type specimen was found.

Distribution: South Africa: Mpumalanga.

Hosts: Unknown.

Chimaerolelaps Desjardins, New Genus

(Fig. 59)

Type Species: *Chimaerolelaps villosa* Desjardins, New Species

Diagnosis: *Chimaerolelaps* is unique among diparines in 2 ways. First, it has 3 pairs of scutellar bristles, while all other diparines have at most 2 pairs. Second, it has an elongate anellus which is at longer than broad (Fig. 59), while all other diparines have an anellus that is broader than long (Figs. 56, 57). *Chimaerolelaps* may superficially resemble *Lelaps* or *Netomocera*. *Chimaerolelaps* has a clypeal margin which is protruding and straight, while *Lelaps* has a median clypeal tooth. *Chimaerolelaps* also has a symmetrical flagellum, while the flagellum in *Netomocera* is asymmetrical.

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Description: Female. *Head:* Occipital margin rounded; occipital carina present; upper face without strong, transversely carinate sculpture; eyes not posteriorly extended beyond occipital margin; inner eye margins uniformly convex; eyes bare; scrobe present and scrobal channel parallel-sided dorsal to toruli; dorsal margin of scrobe rounded; toruli not on shelf, junction of upper and lower face rounded; antennae symmetrically clavate; antennal formula 11173; anellus longer than broad; pedicel, first funicular segment, second funicular segment subequal in length; claval apex without thick tuft of micropilosity; apical clypeal margin protruding and straight; malar groove present; single pair of strong, dark bristles on vertex present. *Mesosoma:* dorsum of mesosoma with strong, dark bristles (1 pair median scutal, 1 pair lateral scutal, 2 pairs anterior scutellar, 1 pair posterior scutellar); pronotum short, collar-like; notauli not arched and meeting posterior scutal margin at lateral edge of scutoscutellar suture; lateral lobes of scutum similar in color to remainder of scutum; posterior scutal margin without setose groove; scutellum large, convex, and sharply sloped posteriorly; axillae convex and not reduced; posterior notal wing process present, pointed; frenum present; metanotum present as narrow, sculptured band; propodeum at least 1.5X longer than high; propodeum with dorso-ventrally flattened spine near anterior margin; plicae absent; suture between postspiracular area and metapleuron diagonal; propodeal foramen circular, open in one plane; mesepisternal depression absent; prepectus elongate, reaching tegula; tegula normal, flap-like; subalare not visible; acropleuron normal, not expanded; mesopleuron with smooth and sculptured regions posteriorly; metacoxa posteriorly convex, with transverse striations; metacoxa posteriorly without thick vertical brush of setae; 2

metatibial spurs, <1.5X width of tibia at point of insertion. *Metasoma:* Petiole

cylindrical, with single pair of setae, at least 2X as long as broad; GT1 expanded,

covering at least half of metasoma length; GT1 rounded lateral to petiole insertion; cercal

setae elongate; cercal brush present. **Male:** Unknown.

Discussion: *Chimaerolelaps* is positioned phylogenetically as sister-group to the *Dipara*

clade, although the only synapomorphy for this clade is the presence of petiolar setae in

the female.

Etymology: *chimaero-*, to represent the odd assemblage of ancestral and derived features

present in this taxon, and *-lelaps*, to ally the genus with Diparinae. The genus is identified

in some collections with a manuscript name. As the manuscript name was somewhat

misleading with regards to the phylogenetic position of the group, it is not used here.

Number of Species: 1 described species.

Distribution: Costa Rica.

Hosts: Unknown.

Key to Species: none.

Chimaerolelaps villosa Desjardins, New Species

(Fig. 59)

Type information: Holotype female (CNC): "Costa Rica, B. Carrillo N. P., 84°07'W; 10°10'N, 10.IV.85; 500m., H. Goulet-L. Masner." 4 paratype females (3 in CNC, 1 in USNM): same data.

Description: Female. 3.8 mm. *Color:* Orangish brown, with the following exceptions: clava whitish yellow gradually darkening to brown funicle; clypeus orange; posterior margin of scutum between notauli black; pro- and metacoxa off-white; distal half of metatibia brown; forewing with 3 brown, irregular, longitudinal bands emanating from distal end of submarginal vein, medial portion of marginal vein, and postmarginal vein, brownish yellow shaded areas present between bands; posterior margin of GT1, dorso-posterior margin of GT2-5, GT6 brown; GT7 off-white; ovipositor off-white proximally gradually darkening to brown distally. *Head:* Subrectangular in frontal view, about 1.1X wider than high; areolate, becoming transversely striate on lower face, striae angling toward clypeus; ratio of ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 2.2: 4.2: 2.4: 1; scrobe high, reaching ventral margin of midocellus; scrobal basin transversely striate-areolate ventrally, becoming areolate dorsally, scrobal walls transversely areolate; interantennal carina strong, reaching about 0.4X height of scrobe; toruli separated by 1.6 torulus diameters; antennae clavate; scape height about 0.9X eye height; anellus about 1.2X longer than broad; ratio of scape: pedicel: anellus: F1: F2: F3 about 7.7: 2: 1: 2.4: 2: 1.8; F4 and F5 about as broad as long;

clypeus well delimited. *Mesosoma:* Pronotum irregularly transversely striate-rugulose,

scutum scabrous, scutellum antero-medially scabrous, laterally and posterior to frenum

with strong longitudinal carinae; ratio of pronotum: scutum: scutellum: propodeum about

1.2: 1.9: 2.1: 1; mesosoma dorsally covered in thick, off-white setae; pronotum 2.1X

wider than long; scutum 1.9X wider than long; marginal rim of scutellum with wide,

upturned carina; metanotum narrow band with pits delimited by longitudinal striae;

propodeum anteriorly with strong, dorso-ventrally flattened spine, with irregularly

longitudinal carinae emanating from spine posteriorly and a single median carina

emanating anteriorly; propodeum becoming areolate lateral to posterior longitudinal

carinae; nucha wide, raised, roughly sculptured band; plicae absent; postspiracular sulcus

deep, with irregular pits divided by transverse carinae; spiracle 1.6X own diameter from

metanotum; callus areolate, with fine, white setae, projecting posteriorly into as spine

lateral to spiracle; prepectus triangular, not in same plane as pronotum, abutting at about

135º angle; mesepimeron smooth with 2 longitudinal depressions with pits divided by

transverse carinae; femoral depression deep, narrow, parallel-sided, with pits delimited

by transverse carinae, well defined anteriorly and posteriorly; metapleuron areolate; pro-

and mesocoxa with sparse white setae on anterior margins, metacoxa with sparse, white

setae on disto-anterior margin; meso- and metatibia spinose; longer metatibial spur about

1.2X length of shorter spur, about 0.7X width of metatibia at point of spur insertion;

metabasitarsus about 4.4X as long as wide, about 0.4X length of remaining tarsi; hind

coxa distinctly transversely striate; macropterous; ratio of submarginal vein: marginal

vein: postmarginal vein: stigmal vein 5.8: 3.2: 1.8: 1; entire wing (including speculum

and basal cell) densely setose. *Metasoma:* About 1.4X length of mesosoma; petiole 2.1X

longer than broad, coriaceous; ratio of GT1: GT2-6:GT7:ovipostor sheaths about 3.9:2.3:1.7:1; GT2-4 dorsally with single pair of long, fine, erect setae; GT3-4 dorso-laterally and GT5 dorsally with row of sparse, white setae; GT6 bare; GT47 and ovipositor sheath with dense white setae; ovipositor apico-dorsally obscured by sheath.

Male: Unknown.

Etymology: *villos-*, meaning hairy, in reference to the thick, white seate convering the dorsal surface of the mesosoma in this species.

Distribution: Costa Rica.

Hosts: Unknown.

Conodipara Hedqvist

Turneria Hedqvist 1969: 177. Type species: *Turneria scutellata* Hedqvist (orig. desig. and by monotypy). [Preoccupied]

Conodipara Hedqvist 1972: 58. [Replacement name for *Turneria*, preoccupied by *Turneria* Forel 1895].

Diagnosis: Both sexes of *Conodipara* can be easily identified based on two autapomorphic features. First, *Conodipara* has a pair of projections on the dorso-lateral surface of the nucha. Second, *Conodipara* has an L-shaped petiole, which is bent downward at 90°. No other diparines possess either of these features.

Discussion: In the phylogenetic analysis, *Conodipara* + (*Conophorisca*, *Myrmicolelaps*) was recovered as monophyletic based on 5 synapomorphies: the loss of sexual dimorphism, filiform antennae, a 2-segmented clava, posterior surface of mesopleuron heavily sculptured, and presence of a long petiole. *Conodipara* is also basal in a two-branch clade in which *Pyramidophoriella* occupies the basal position in the other branch. This clade was united by 3 synapomorphies, which include a conical scutellum, a reduced metanotum, and a posteriorly rising propodeum.

Number of Species: 1 described.

Distribution: South Africa (Eastern Cape).

Hosts: Unknown.

Species of *Conodipara*:

scutellata (Hedqvist). AFROTROPICAL: South Africa.

> *Turneria scutellata* Hedqvist 1969: 176-178 (Fig. 2). Holotype female: S. Africa, Pondoland, Port St. John, Jan. 1924. coll. R. E. Turner. (BMNH, examined). 29 Paratype females and 21 Paratype males: S. Africa, Pondoland, Port St. John, Jan 1924 (6 females, 6 males), 6-25 Feb. 1924 (15 females, 4 males), 1-17 Mar. 1924 (2 females, 4 males), 29.I.-5.II.1924 (6 females, 6 males) and Nov. 1923 (1 male). coll. R. E. Turner. (BMNH, examined).

Conophorisca Hedqvist

(Figs. 5-15, 60, 61)

Conophorisca Hedqvist 1969: 199-201. Type species: *Conophorisca annulata* (orig.

desig. and by monotypy).

Diagnosis: *Conophorisca* belongs to a clade with *Myrmicolelaps*, and this clade can be

diagnosed with 2 characters. First, the propodeal foramen is hinge-like, opening both

dorsally and ventrally (Fig. 31). All remaining diparines have a propodeal foramen

which is circular and open only in 1 plane. Second, the petiole is at least 2X as long as

broad and constricted antero-ventrally (Fig. 12). Few diparines have petioles more than

1.5X as long as broad, and all other diparines have a cylindrical petiole (Fig. 57), or in

the case of *Conodipara*, an L-shaped petiole. Within this clade, *Conophorisca* can be

identified by having its toruli located on a shelf, where the upper face is separated from

the lower face by a sharp angle of ~90° (Fig. 8), and also by lacking an expanded axillary

wing sclerite (Fig. 10, see Fig. 30 for presence of the sclerite).

Discussion: *Conophorisca* is not resolved as monophyletic in the phylogenetic analysis

(the three species form an unresolved polytomy with *Myrmicolelaps*). The combined

clade is supported by a the presence of a hinge-like propodeal foramen and an antero-

ventrally constricted petiole. However, *Conophorisca* itself may actually represent a

monophyletic lineage. The three characters which would support *Conophorisca*

paraphyly are eye setation, presence/absence of a malar groove, and degree of claval

fusion. The difficulty of coding eye setation is discussed in that character's entry (#12). Regarding the malar groove and claval fusion, it is possible that reduction of the groove and fusion of all claval segments may be associated with a reduction of body size. *Conophorisca grisselli* is extremely small, and has both of these features, while the larger *C. annulata* and *C. littoriticus* have a malar groove and only 2 fused claval segments. On the other hand, the presence of a sharply angled torular shelf supports monophyly of the genus. While the previously mentioned characters are highly homoplastic in the analysis (e.g. setose eyes are independently derived 6 times), the torular shelf in only derived independently in one other taxon, *Dozodipara*. *Conophorisca* is maintained as a valid genus herein, because of its potential monophyly and its lack of the multiple synapomorphies uniting *Myrmicolelaps* (these characters are discussed under the generic entry for *Myrmicolelaps*).

Number of Species: 3 described, at least 3 undescribed.

Distribution: South Africa (Western Cape, Eastern Cape).

Hosts: Unknown.

Key to Species: Given below.

Key to the species of *Conophorisca* Hedqvist

1.   Occipital margin carinate; antenna elongate (F1 about 1.5X length of pedicel);
clava 1-segmented; without metallic highlights on vertex

annulata Hedqvist

Occipital margin rounded; antenna more compact (F1 subequal in length to
pedicel); clava 1- or 2-segmented; with or without metallic highlights on vertex

2

2.   Malar groove present; clava 2-segmented; with metallic highlights on vertex

littoriticus Desjardins,

new species

Malar groove absent; clava 1-segmented; with or without metallic highlights on

vertex   *grisselli* Desjardins, new

species

Species of *Conodipara*:

annulata Hedqvist. AFROTROPICAL: South Africa.

Conophorisca annulata Hedqvist 1969: 199-201 (Fig. 19). Holotype female: E.
Cape Prov., Katberg, 4,000 ft, 1-15.I.1933, leg. R. E. Turner (BMNH, examined).
Unknown number of paratype females: Cape Prov., Mossel Bay, Aug. 1924, leg.
R. E. Turner (KHPC, not examined).

Conophorisca littoriticus Desjardins, New Species

(Fig. 61)

Type Information: Holotype female (SAM) "South Africa, W. Cape, Walker Bay

Nature Res., 34°27.41'S 19°21.39'E, 4 Oct-1 Nov 1997, S. van Noort and B. Fisher,

WA97-Y63, Pitfall trap, Station 3, South Coast Strandveld, dominated by *Indigofera*

brachystachya E. May." Paratypes: 2 males (same data except 1 specimen: 26 Dec - 24

Jan), 2 females (same data except 1 specimen: 17 May – 14 Jun, 1 specimen: 9 Aug – 6

Sep).

Description: Female. 2.6 mm. *Color:* Orangish brown to dark orangish brown with the

following exceptions: Head brownish metallic green on upper face and vertex, gena

brown, scape (except distal tip) brownish white, distal tip of scape, pedicel brown,

anellus, F1 brownish white, F2 brownish white proximally to brown distally, remaining

flagellar segments brown, distal 2/3 of procoxa and distal 1/2 of metacoxa white, femoral

depression, mesepimeron, metapleuron, and dorso-posterior region of metacoxa with

metallic green and blue highlights, gaster brown. *Head:* Subquadrate in frontal view,

1.1X as wide as high; eye bare, 1.5X as high as wide; head finely coriaceous; ocellocular:

postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 3.1:6:2.9:1;

scrobe high, triangular, and deep, reaching from torulus to midpoint on mid-ocellus (mid-

ocellus partially in scrobe); scrobal basin and walls coriaceous-transversely striate;

interantennal carina strong, reaching about 1/3 height of scrobe; toruli separated by

slightly less than 1 torulus diameter; scape about equal to eye height; anellus reduced and

partially fused to F1, 4.5X broader than long; ratio of scape: pedicel: anellus+F1: F2: F3 about 5.5:1.5:1.6:1.2:1, F4-7 each about as wide as long; clava 2-segmented, with segments 2 and 3 fused; malar sulcus absent, although faint sculptured depression present; clypeus strongly delimited laterally, finely delimited dorsally; clypeal margin bilobed. *Mesosoma:* Dorsally coriaceous; ratio of pronotum: scutum: scutellum: propodeum about 4.3:1:1.6:4.2; pronotum about 1.1X as wide as long; scutum 4x as wide as long; posterior scutellar margin smooth; metanotum smooth, polished band; propodeum coriaceous-striate; plicae absent; postspiracular sulcus wide and shallow, crossed by 2-3 transverse carinae; spiracle about 5X its own diameter from metanotum; spiracle facing postero-laterally; prepectus subtriangular, in same plane as pronotum; acropleuron and mesepisternum coriaceous, mesepimeron transversely striate; femoral depression well defined, anterior 1/2 of depression alveolate, posterior 1/2 transversely striate; anterior 2/3 of metapleuron coriaceous, posterior 1/3 alveolate; metapleuron fused to propodeum anterior to propodeal spiracle; meso- and metatibia ventro-distally spinose; one metatibial spur, 1.3X width of metatibia at point of insertion; metabasitarsus about 6.4X as long as wide, about 0.7X length of remaining tarsi; posterior margin of metacoxa distinctly transversely striate; metacoxa without setae; apterous, forewing reduced to small membranous area, hindwing apparently absent. *Metasoma:* 1.2X length of mesosoma; petiole about 1.6X as long broad, posterior 3/4 transversely striate, anterior 1/4 smooth; ratio of GT1: GT2-6: GT7: ovipositor sheaths about 19:1:2.3:3.3; GT1 dorsally covered with sparse, white setae (separated by 1-3X setal length),GT2-5 latero-ventrally with row of white setae, GT6-7, ovipositor sheaths covered in white setae; ovipositor smooth and pointed. **Male:** Same as female.

Etymology: *littor-*, meaning shore, for the coastal strandveld habitat in which the specimens were collected.

Distribution: South Africa (Western Cape Province).

Hosts: Unknown.

Conophorisca grisselli Desjardins, New Species

(Figs. 5-15, 60)

Type information: Holotype female (SAM) "South Africa, W Cape, Koeberg Nature Reserve, 33°37.62'S 18°24.26'E, 28 Nov-27 Dec 1997, S. van Noort, K097-Y137, Yellow Pan trap (cup), Station 2, West Coast Strandveld dominated by *Euphorbia* and *Rhus* spp." Paratypes: 5 males, 5 females (same data as holotype).

Description: Female. 1.8 mm. *Color:* Brownish orange with the following exceptions: Vertex dark brown to metallic blue, upper face and gena brow, lower face orangish brown, pro- and metacoxa orangish white, legs orangish yellow, petiole light brown, remaining metasoma brown. *Head:* Subtriangular-ovate in frontal view, slightly wider than high (1.1:1); eyes bare, 1.4X as high as wide; vertex smooth, remaining head finely coriaceous; ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 2.3:5.7:3.3:1; scrobe high, narrow, deep, reaching from torulus to ventral margin of mid-ocellus; scrobal basin transversely striate, scrobal walls coriaceous-striate; interantennal carina strong, reaching 0.4X height of scrobe; toruli separated by about 1

torulus diameter; scape length about equal to eye height; anellus reduced and partially fused to F1, 2-3X as broad as long; ratio of scape: pedicel: anellus+F1: F2: F3 about 5.3:1.3:1:1:1, F4-7 each about 2X as long as wide; clava 1-segmented, all segments fused; malar sulcus absent; clypeus strongly delimited laterally, finely delimited dorsally; clypeal margin symmetrically sinuate. *Mesosoma:* Dorsally smooth to coriaceous; ratio of pronotum: scutum: scutellum: propodeum about 3.4:1:1:3.1; pronotum about as wide as long; scutum 2.7X as wide as long; posterior scutellar margin smooth; metanotum smooth, polished band; propodeum coriaceous anteriorly to smooth posteriorly; plica absent; postspiracular sulcus wide, shallow, and smooth; spiracle about 3.4X its own diameter from metanotum; spiracle facing postero-laterally; prepectus triangular, in same plane as pronotum; acropleuron mostly smooth, slightly coriaceous, mesepisternum coriaceous, mesepimeron smooth to rough-coriaceous; femoral depression distinct, coriaceous-alveolate; metapleuron coriaceous anteriorly to smooth posteriorly; metapleuron not fused to propodeum, although sulcus weaker anterior to spiracle; meso- and metatibia ventro-distally spinose; one metatibial spur, 0.9X width of metatibia at point of insertion; metabasitarsus about 4.8X as long as wide, about 0.6X length of remaining tarsi; posterior margin of metacoxa faintly transversely striate; metacoxa without setae; apterous, forewing reduced to small membranous area, hindwing apparently absent. *Metasoma:* 1.2X length of mesosoma; petiole about 1.7X as long as broad, roughly sculptured; ratio of GT1: GT2-6: GT7: ovipositor sheaths about 15:4.7:1:2.3; GT1 dorsally covered with sparse, white setae (separated by 2-3X setal length),GT2-6 latero-ventrally with rows of white setae, GT7, ovipositor sheaths covered in white setae; ovipositor tip smooth and pointed. **Male:** Same as female.

Etymology: Named for my co-advisor, E. Eric Grissell, whose guidance was invauable in the completion of the morphological component of my dissertation.

Distribution: Costa Rica.

Hosts: Unknown.

Dipara Walker

Dipara Walker 1833: 371, 373. Type species: *Dipara petiolata* Walker (by monotypy).

Tricoryphus Forster 1856. [Synonomized by Domenichini 1953]

Apterolelaps Ashmead 1901. [Synonomized by Delucchi 1959; Heydon and Boucek 1992]

Alloterra Kieffer and Marshall 1904: 46-47. Type species: *Alloterra claviger* Kieffer and Marshall (by monotypy). **New synonymy.** [Type specimen of genus not examined]

Trimicrops Kieffer 1906. [Synonomized with *Alloterra* by Dessart 1996]

Parurios Girault 1913: 318. Type species: *Parurios australiana* Girault (by monotypy). [Boucek stated the original description as 1913[175], but it appeared earlier in 1913[169]]. **New synonymy.** [Type specimen of genus not examined]

Epilelaps Girault 1915: 344. Type species *Epilelaps hyalinipennis* Girault (by orig. desig.). [Synonomized by Boucek 1988]

Pseudipara Girault 1915: 345. Type species: *Pseudipara albiclava* Girault (orig. desig. and by monotypy). **New synonymy.** [Type specimen of genus examined]

Uriolelaps Girault 1915: 201. Type species: *Uriolelaps argenticoxae* Girault (orig. desig.) [Synonomized with *Parurios* by Boucek 1988].

Hispanolelaps Mercet 1927. [Synonomized by Domenichini 1953]

Pseudiparella Girault 1927: 334-335. Type species *Pseudiparella emersoni* Girault (by monotypy). [Synonomized by Boucek 1988]

Emersonia Girault 1933: [1]. Type species: *Emersonia atriscutum* Girault (by monotypy). [Synonomized with *Parurios* by Boucek 1988]

Grahamisia Delucchi 1962: 379-380. Type species: *Grahamisia saetosa* Delucchi (orig. desig. and by monotypy). **New synonymy.** [Type specimen of genus not examined]

Afrolelaps Hedqvist 1963: 47. Type species: *Afrolelaps maculata* Hedqvist (orig. desig.). [Synonomized by with *Grahamisia* by Hedqvist 1969]

Pondia Hedqvist 1969: 197. Type species: *Pondia punctulata* Hedqvist (orig. desig.). **New synonymy.** [Type specimen of genus examined]

Diparomorpha Hedqvist 1971: 57-58. Type species: *Diparomorpha machadoi* Hedqvist (orig. desig. and by monotypy). **New synonymy.** [Type specimen of genus notexamined]

Diagnosis: *Dipara* females can be identified by a combination of features. First, at least one pair of setae (or bristles; Fig. 53) are present on the lateral margins of the petiole. The only other females with these setae are *Chimaerolelaps*, *Lelaps*, and *Neapterolelaps*. *Dipara* is distinguished from *Chimaerolelaps* by an anellus that is broader than long and at most 2 pairs of scutellar bristles. *Chimaerolelaps* has an anellus that is longer than

broad and 3 pairs of scutellar bristles. *Dipara* can be distinguished from *Lelaps* by the

absence of a median clypeal tooth, which all species of *Lelaps* have. Finally, *Dipara* can

be easily distinguished from *Neapterolelaps* by the characteristics discussed in the

diagnosis for *Neapterolelaps*. *Dipara* males can be separated from *Lelaps* males by their

lack of a median clypeal tooth. They can be distinguished from *Netomocera* males by

their elongate petiole (>2X longer than broad, whereas *Netomocera* males have a petiole

that is broader than long.

Discussion: Delucchi (1959) first proposed that *Apterolelaps* Ashmead was a synonym

of *Dipara* Walker (as *Tricoryphus* Forster). Later, both Hedqvist (1969) and Yoshimoto

(1977) treated *Apterolelaps* as a valid genus based on the absence of an anellus.

However, Heydon and Boucek (1992) resynonymized *Apterolelaps*, suggesting that the

type specimen was aberrant in having a partially fused anellus. Heydon and Boucek then

stated that Yoshimoto's (1997) description of *Dipara pedunculata* matched *Apterolelaps*,

although the type specimen he selected differed from the description and appeared

identical to *Dipara canadensis* Hedqvist. Heydon and Boucek therefore synonomized

Dipara pedunculata Yoshimoto with *Dipara canadensis* Hedqvist. Additionally,

although *Tricoryphus* Forster and *Hispanolelaps* Mercet were technically synonymized

by Domenichini (1953), Boucek (1954) stated that this was discovered by S. Novitzky,

and Domenichini published these results without crediting him.

     Dipara sensu Boucek (1988) and groups of taxa which appeared intermediate to

Dipara and *Parurios* were divided into multiple taxonomic units for the phylogenetic

analysis, which are discussed in the *Taxonomic Scope* section. In the following

discussion, these taxonomic units are referred to in quotation marks, so as not to mistake them for valid names. Dipara was resolved as a paraphyletic grade in the phylogenetic analysis based, the entire clade of which is based on 3 synapomorphies: female petiole with setal pairs, male flagellar segments pedunculate, and male flagellar segments with appressed setae. The following genera render *Dipara sensu* Boucek (1988) paraphyletic and are herein in synonymized with Dipara: *Alloterra* Keiffer, *Grahamisia* Delucchi, *Parurios* Girault, and *Pseudipara* Girault. *Pondia* also renders *Dipara* paraphyletic, and the retention of *Pondia* as a generic level taxon is explained in its generic entry. Within this revision, the reasoning behind synonymy is generally given before the synonymy itself. However, the situation with *Dipara* is so complex that it is important to provide an overview before examining the specific details.

It should also be noted that synonymies in this revision are generally made on phylogenetic grounds, i.e. multiple genera are strongly supported as a monophyletic group, in addition to general morphological similarity. However, the synonymy of genera within *Dipara* is done more on utilitarian grounds, although phylogeny still plays an important role. It is impossible to separate these genera into monophyletic taxa for which both females and males are diagnosable. Additionally, variation in the arrangement of the taxa across analyses makes it difficult to ascertain what these monophyletic divisions might be. The obvious alternative to massive paraphyletic synonymy is to leave the classification of these genera the way it is. However, this would involve ignoring a tremendous amount of information gathered during this study. This information includes the fact that approximately ¼ of all female specimens within this clade found in museum collections are unidentifiable given the current generic

definitions, the fact that *Alloterra* and *Parurios* males are indistinguishable where their ranges overlap, and the fact that an obviously conspecific collection of females and males from Tanzania has females easily classifiable as *Dipara s. s.* and males easily classifiable as *Parurios*. Therefore, the taxonomic utility gained in these synonymies outweighs the erection of a genus which is most likely paraphyletic. Additional reasons for the synonymy of each genus within *Dipara* are discussed below.

Grahamisia Delucchi is extremely similar to *Dipara sensu stricto*, and in many museum collections the former is listed as a synonym of the latter, although the two have never been formally synonomized. Boucek (1988) maintained *Grahamisia* as a valid genus, although he stated that further examination of the African fauna may lead to its synonymy. *Grahamisia* and *Dipara sensu stricto* group together in all analyses based on 2 synapomorphies: a laterally bulging pronotum and a heavily sculptured mesepimeron. *Grahamisia* differs from *Dipara sensu stricto* only in notaular structure and the presence of black circular markings on the lateral lobes of the scutum. *Grahamisia* also renders *Dipara sensu* Boucek (1988) paraphyletic in the phylogenetic analysis, and for these reasons it is synonomized with *Dipara*.

Boucek (1988) maintained *Pseudipara* Girault as a genus, presumably for two reasons. First, it has a more slender habitus than *Dipara*, and second, it has a much longer petiole. In the phylogenetic analysis *Pseudipara* renders *Dipara sensu* Boucek (1988) paraphyletic, and groups with *Alloterra* and "Micro Dipara" based on having notauli which meet the posterior scutal margin close together but are not strongly arched. Due to the lack of qualifiable morphological differences between *Pseudipara* and *Dipara*

and the phylogenetic positioning of *Pseudipara*, *Pseudipara* is synonomized with *Dipara*.

Additionally, both *Parurios* Girault and *Alloterra* Kieffer rendered *Dipara sensu* Boucek (1988) paraphyletic in the phylogenetic analysis. Unlike the majority of diparine genera, *Dipara sensu* Boucek (1988) and *Parurios* have traditionally been separated by male morphology. In the majority of keys (e.g., Boucek 1988), the males of both *Alloterra* and *Parurios* are identified by their short, cylindrical flagellar segments with short setae while *Dipara s. s.* has long, pedunculate segments with long setae. Since *Alloterra* and *Parurios* have not been thought to overlap in distribution, and since the antennal structure has been thought to be a reliable separator of *Dipara sensu* Boucek (1988) and *Parurios*, this has seemed effective. However, both *Alloterra* and *Parurios* are present in Central America, and this had lead to the misidentification of many neotropical *Parurios* males as *Alloterra* and *Parurios* females as *Dipara*. Thus, the male of *Alloterra* is indistinguishable from the male of *Parurios*, and other than geographically the two genera have limited overlap. Also, a diparine species from Tanzania was examined that appears to have typical *Dipara sensu stricto*-like females and typical *Parurios*-like males. Although the specimens were not reared, and therefore no certain association can be made, the simultaneous collection of a large series of both sexes and strong similarities in mesosomal sculpture suggest they are conspecific. Therefore, the cylindrical antennae may not be as reliable an indicator as previously thought.

Alloterra and *Parurios* are not resolved as sister-taxa in any of the phylogenetic analyses. Additionally, molecular evidence (Desjardins et. al., in prep) supports a sister-group relationship between *Alloterra* and "Australian Dipara" rather than one between

Alloterra and *Paurios*. In the molecular analysis, *Alloterra* and "Australian Dipara" are shown as sister-groups, with *Parurios* sister to that clade, and have much higher sequence similarity to each other than either does to *Parurios*. While this information in itself could suggest that the pedunculate antennae of *Dipara* is derived relative to the cylindrical antennae of *Alloterra* and *Parurios*, character state reconstruction shows that *Dipara*-like antennae are the ancestral state for the entire clade.

Boucek (1988) separated the females of *Dipara* from *Parurios* based on the position of the median scutal bristles. However, he noted that this character system only worked with the Australian fauna, as non-Australian *Dipara* would be identified as *Parurios* in his key. No character was found that would reliably separate female *Parurios* from *Dipara sensu* Boucek (1988) at the world level, and if antennal morphology is as is plastic as the previous discussion suggests, there is no reliable way to separate these groups in either sex. For these reasons, *Parurios* is synonomized with *Dipara*.

The female of *Alloterra* Kieffer is a highly modified, minute, apterous diparine with reduced eyes and no ocelli. However, as previously mentioned, the phylogenetic analysis supports its position within *Dipara sensu* Boucek (1988), and the male of *Alloterra* is indistinguishable from *Parurios*-like males. (It should be noted that Yoshimoto (1977) keyed the male of *Alloterra* based on the presence of a spur on the posterior surface of the metacoxa. However, this spur is actually an extension of the lower-most metacoxal striation, and occurs to varying degrees throughout both *Dipara sensu* Boucek (1988) and *Parurios*-like males.) For the aforementioned reasons, *Alloterra* is herein synonomized with *Dipara*.

Pondia Hedqvist either is nested within a monophyletic *Dipara* or lies at the base of the clade containing the most derived diparines, depending on the analysis. When in the latter position, the clade of *Pondia* Hedqvist + the derived diparines is supported by 3 synapomorphies: a reduced prepectus, reduced axillae, and the loss of the median scutal bristles. The reduction of the prepectus and axillae may play a functional role in the further specialization of diparines to litter habitats; none of the diparines within clade inclusive of *Pondia* have winged females (or even brachypterous females). Regardless, *Pondia* Hedqvist renders *Dipara* paraphyletic in all analyses and the former herein synonymized with the latter.

Diparomorpha Hedqvist is the one described diparine genus not included in the phylogenetic analysis, as it is known only from the type specimen which could not be located. Hedqvist denoted a variety of depositories for his types throughout his descriptions, including his own personal collection. However, most of his holotypes are housed at the British Museum of Natural History, regardless of the listed type depository. Two holotypes were acquired through Christer Hanssen (Swedish Museum), *Diparisca ferriei* and *Dipara canadensis*, which were claimed to be the only types remaining in his personal collection. The holotype of *Diparomorpha* (which is known only from the type) is located neither in the BMNH nor in Hedqvist's personal collection. Furthermore, contact could not be established with the Laboratório de Biologia, Dundo, Lunda, Angola, which is the listed depository for the specimen.

From the description and illustrations, it is apparent that *Diparomorpha* belongs in *Dipara*. The former differs from the latter in only two respects. Although Heqvist describes Diparomorpha as having 7 funicular segments and no anellus, his illustration

suggests that an anellus is present. *Diparomorpha* also completely lacks notauli (which appeared to be Hedqvist's justification for describing it as a new genus), which it shares only with *Pyramidophoriella*. However, notaular form is extremely variable in *Dipara* and more broadly in Diparinae, and this likely represents an autapomorphic state within *Dipara*. In addition, *Diparomorpha* possesses an extremely dorsally flattened thorax, and although an illustration in dorsal view is not provided, the description is similar to the thorax of *Dipara turneri* and the taxonomic unit Fijian *Dipara/Parurios*. As both the latter taxa have very fine and weakly impressed notauli, it is possible that notauli were lost entirely by *Diparomorpha* within this clade. Therefore *Diparomorpha* is also synonomized with *Dipara*, and likely occupies a phylogenetic position near the aforementioned taxa.

Number of Species: 36 described species, possibly hundreds of undescribed species.

Distribution: Cosmopolitan.

Hosts: An undescribed Indian species (*Parurios* Girault) was reared from a curculionid (Coleoptera) feeding on the roots of *Cyperus* (Boucek 1988).

Key to Species: None.

Species of *Dipara*:

agenticoxae (Girault). AUSTRALIAN: Australia (Quensland).

> *Uriolelaps agenticoxae* Girault 1915: 201-202. Holotype female: Babinda,
> Queensland, Feb. 5, 1914, jungle, coll. A. P. Dodd. (QM, examined).

albiclava (Girault). AUSTRALIAN: Australia (Queensland).

Pseudipara albiclava Girault 1915: 345. Holotype female: Queensland:

Gordonvale (Cairns), Mt. Pyramid, alt. 2500-3000 ft, forest, sweeping, June 13,

1913, coll. A. P. Dodd. (QM, examined).

albomaculata (Hedqvist). AFROTROPICAL: Angola.

Afrolelaps albomaculata Hedqvist 1963: 47-49 (Figs. 1, 2). Holotype female and

4 female paratypes: [Angola]: Détritus du sol de la R. Cambonde, affl. riv. dr. de

la Uamba (8.5 S., 18.13 E.; alt. 750 m), Mabete, Caungula, 20.VII.1962, coll. A.

de B. Machado. (Holotype and 2 paratypes at LBDA, 2 paratypes at SMNH, not

examined).

atriscutum (Girault). AUSTRALIAN: Australia (Victoria).

Emersonia atriscutum Girault, 1933: [1]. Holotype female: Belgrave, Victoria,

coll. A. P. Dodd. (type location uncertain).

australiana (Girault). AUSTRALIAN: Australia (New South Wales).

Parurios australiana Girault 1913: 318. Holotype female: Ourimbah, New South

Wales. (SAM, not examined).

belokobylskii Dzanokmen. EURASIAN: Russia.

    Dipara belokobylskii Dzanokmen 1993: 103-106. Holotype female: Russia-

    Khabarovsk Kray. (ZISP, not examined).

canadensis Hedqvist. NEARCTIC: Canada and USA.

    Dipara canadensis Hedqvist 1969: 193 (Fig. 13). Holotype female: Canada, Ont.,

    Gatinau Park, 21.V.1967, coll. K.-J. Hedqvist. (KHPC, examined).

    Dipara pedunculata Yoshimoto 1977: 1040-1042 (figs. 21, 27). Holotype female

    and allotype male: 5 mi west of Hopkinsville, KY., 22.IX.67, Berlese sample of

    deciduous duff. coll. J. M. Campbell. (CNC, not examined). 3 male paratypes:

    NC: Duke Forest, 16.IX.44, pine on clay litter. coll. A. S. Pearse (2 males), and

    data unknown, Lot No. 52-2056, 16.IX.51 (1 male). (USNM, examined).

    [Synonomized by Heydon and Boucek 1992]

claviger (Kieffer and Marshall). EURASIAN: Italy.

    Alloterra claviger Kieffer and Marshall 1904: 46-47. Holotype female: Italy.

    Trimicrops claviger Kieffer 1906: 142. Holotype female: Italy. [Synonomized

    with *Alloterra* by Dessart 1996]

conoidea (Xiao and Huang). EURASIAN: China.

> *Parurios conoidea* Xiao and Huang 2000: 331-332. Holotype female: Peoples'
>
> Republic of China-Henan. (IZAS, not examined)

dictyodroma (Xiao and Huang). EURASIAN: China.

> *Grahamisia dictyodroma* Xiao and Huang 1999: 334-335. Holotype female:
>
> Peoples' Republic of China-Hubei. (IZAS, not examined).

emersoni (Girault). AUSTRALIAN: Tasmania.

> *Pseudiparella emersoni* Girault 1927: 335. Holotype female: Tasmania: Wilmot.
>
> coll. A. M. Lea and H. J. Carter. (type location unknown).

fusca (Girault). AUSTRALIAN: Australia (Quennsland).

> *Lelaps fusca* Girault 1915: 200. Holotype male: Gordonvale (Cairns),
>
> Queensland. Jungle, May 18, 1913, A. P. Dodd. (QM, examined). [Transferred to
>
> Parurios by Boucke (1988)].

hyalinipennis (Girault). AUSTRALIAN: Australia (Queensland).

> *Epilelaps hyalinipennis* Girault 1915: 344. Holotype female: Gordonvale
>
> (Cairns), Queensland. Jungle, June 7, 1913. (QM, examined).

keatsi (Girault). AUSTRALIAN: Australia (Queensland).

Uriolelaps keatsi Girault 1922: 41. Holotype female: Fishery Creek, Queensland,

Jungle, June. (QM, examined).

keralensis Narendran & Sureshan. ORIENTAL: India.

Dipara keralensis Narendran & Sureshan, 2001: 452-453 (Figs. 1, 2). Holotype

female (orig. desig.): Parambikulam, Kerala, 2.ix.1995, coll. P. M. Sureshan.

(ZSIC not examined). Paratype female (orig. desig.): Calicut University Campus,

Kerala, 4.ix.2000, coll. T. C. Narendran. (ZSIC not examined).

machadoi (Hedqvist). AFROTROPICAL: Angola.

Diparomorpha machadoi Hedqvist 1971: 57-58. Holotype female: [Angola]:

Enviorns de Dundo: détritus végétaux du sol de la forêt-galerie de la rivière

Dicoco, affluent de la riv. Luachimo (7.25 S., 20.55 E.), 25.XI.1970, coll. A. de

B. Machado and S. A. Peles. (LBDA, not examined).

maculata (Hedqvist). AFROTROPICAL: Angola.

Afrolelaps maculata Hedqvist 1963: 48-50 (Figs. 1, 2). Holotype female:

[Angola]: Détritus du sol de la galerie forestière de la R. Tshihumbuè, affl. de la

rive droite de la R. Lubalo (8.01 S., 19.20 E.; alt. 1000 m). Poste de Camaxilo,

6.VIII.1962. coll. A. de B. Machado. (LBDA, not examined).

malabarensis (Narendran and Mini). ORIENTAL: India.

> *Grahamisia malabarensis* Narendran & Mini 2000: 371-374 (Figs. 1-3). Holotype female: Calicut University Campus, Kerala, India, 2.ii.1997. coll. T. V. Mini. (DZCU, not examined). 1 paratype female: Tiruvannur, Calicut, Kerala, 16.xi.1996. (DZCU, not examined).

miniae Narendran & Sureshan. ORIENTAL: India.

> *Dipara miniae* Narendran & Sureshan 2001: 453-455 (Figs. 3-6). Holotype female (orig. desig. and by monotypy): Chindaki, Kerala, 13.xii.1987, coll. T. C. Narendran and party. (ZSIC, not examined).

mohanae Narendran & Sureshan. ORIENTAL: India.

> *Dipara mohanae* Narendran & Sureshan 2001: 455-456 (Figs. 7, 8). Holotype female (orig. desig. and by monotypy): Thiruvannur, Kozhikode, Kerala, 16.xi.1996, coll. K Raj Mohana. (ZSIC, not examined).

nigriceps (Ashmead). NEARCTIC: USA (West Virginia).

> *Apterolelaps nigriceps* Ashmead 1901: 312. Holotype female: USA, West Virginia. (USNM, examined)

> *Apterolaelaps nigriscutum* Girault 1916: 264. [Gahan and Fagan (1923) stated that Girault's species was isotypic with Ashmead's.]

nigrita Hedqvist. AFROTROPICAL: Congo.

> *Dipara nigrita* Hedqvist, 1969: 195 (Fig. 16). Holotype female: Congo, Mount Kabobo, Terr. Albertville, Hte. Kiymbi, 1700 m, X.1958, coll. N. Leleup. (MRAT, not examined).

nigrofasciata Hedqvist. AFROTROPICAL: Madagascar.

> *Dipara nigrofasciata* Hedqvist 1969: 194-195 (Fig. 15). Holotype female: Madagascar: Mandraka, I.1944, coll. A. Seyrig. (MRAT, not examined).

palauensis Yoshimoto & Ishii. OCEANIAN: Micronesia.

> *Dipara palauensis* Yoshimoto & Ishii 1965: 165-166 (Fig. 29). Holotype female: Ngerchelong, Babelthuap I., Palau, Dec. 18, 1947, coll. Dybas. (USNM, examined). Paratype female: Mt. Unibot, Ton I., Truk, Feb. 4, 1953, coll. Gressitt. (BISH, not examined).

pallida (Hedqvist). AFROTROPICAL: South Africa.

> *Pondia pallida* Hedqvist 1969: 198-199 (Figs. 17, 18). Holotype female: S. Africa, Pondoland, Port St. John, Jan. 1924, coll. R. E. Turner. (BMNH, examined). 12 female paratypes: S. Africa, Pondoland, Port St. John, Jan. 1924, coll. R. E. Turner (7 females), and 29.I-5.II 1924, coll. R. E. Turner (5 females). (BMNH and KHPC, examined).

petiolata Walker. EURASIAN: United Kingdom.

> *Dipara petiolata* Walker 1833: 65. [Lectotype female (United Kingdom:
>
> England, BMNH, examined) designated by Graham (1969).]

> *Dipara cinetoides* Walker 1834: 166. [Synonymized by Graham (1967).]

> *Tricoryphus fasciatus* Thomson 1876: 54. Holotype female: Sweden. (LUZN, not
>
> examined) [Synonymized by Boucek (1954).]

> *Hispanolelaps coxalis* Mercet 1927: 62. Holotype female: Spain. (IEEM, not
>
> examined) [Synonymized by Dominichi (1953).]

ponderosa (Girault). AUSTRALIAN: Australia (Queensland).

> *Epilelaps ponderosa* Girault 1915: 344. Holotype female: Gordonvale (Cairns),
>
> Queensland. Jungle, June 16, 1913. (QM, not examined).

poei (Girault). AUSTRALIAN: Australia (New South Wales).

> *Uriolelaps poei* Girault 1915: 202. Holotype female: Tween Heads, New South
>
> Wales, jungle, Tween River, May 2, 1914, coll. A. P. Dodd. (QM, examined).

punctulata (Hedqvist). AFROTROPICAL: South Africa.

> *Pondia punctulata* Hedqvist 1969: 197-198 (Figs. 17, 18). Holotype female: S.
>
> Africa, Pondoland, Port St. John, Jan. 1924, coll. R. E. Turner. (BMNH,

examined). 4 female paratypes: S. Africa, Pondoland, Port St. John, Jan. 1924,

coll. R. E. Turner (3 females), S. Africa, Pondoland, Port St. John, 1-17 Mar.

1924, coll. R. E. Turner (1 female). (BMNH and KHPC, examined).

rufescens Masi. AFROTROPICAL: Seychelles Islands.

Dipara rufescens Masi 1917: 186-188. Holotype female: "Mahé: marshy coastal

plain near Anse Royale.-Silhoutte: coast near Pointe Etienne, and forest above

Mare aux Cochones.-Félicité Island." (BMNH, examined) [member of *Parurios*

clade rather than *Dipara sensu* Boucek (1988)].

saetosa (Delucchi). AFROTROPICAL.

Grahamisia saetosa Delucchi 1962: 380-383 (Figs. 18, 19). Holotype female and

1 paratype female: Tanganyika Terr., Mt. Oldeani, versant Est. 2350-2500 m., 6-9

juin 1957, forêt bambous. (MRAT, not examined). 2 female paratypes: Mt.

Hanang, versant Sud, 2400-2600 m., 24 mai 1957, forêt de montagne avec

Juniperus. (MRAT, not examined). 1 female paratype: Mts. Uluguru, sommet du

kidunda, 1800-1950 m., 3 mai 1957, forêt de montagne. (DPC, not examined).

straminea (Hedqvist). AFROTROPICAL.

Grahamisia straminea Hedqvist 1969: 187-188 (Figs. 10, 11). Holotype female:

Kivu, Terr. Mwenga, S.-O. Tombwe. Lulko, 2100 m (for mont.), I, 1952, coll. N.

Leleup. "Récolté dans l'humus". (MRAT, not examined).

striata (Hedqvist). AFROTROPICAL: South Africa.

>*Grahamisia striata* Hedqvist 1969: 188 (Fig. 12). Holotype female: S. Africa,
>
>Cape Prov. Sumerset, 1-26.i., 1931, coll. R. E. Turner. (BMNH, examined).

trilineatus (Yoshimoto).

>*Trimicrops trilineatus* Yoshimoto 1977: 1038 (Fig. 19). Holotype female:
>
>Edmonson Co., Mammoth Cave Nat'l. Park, Kentucky, 24.III.73, W. Suter (CNC
>
>No. 15003, not examined).

>*Trimicrops bilineatus* Yoshimoto 1977: 1037-1038 (Figs. 1, 8, 25). Holotype
>
>female: Williamsville, Missouri , 12.VII.55, E. C. Becker, Berlese sample,
>
>deciduous duff. Allotype male: Williamsville, Mo., 25.VII-15.VIII.69 (CNC No.
>
>15002, not examined). [Synonymized by Boucek 1993]

truncatipennis (Dodd). AUSTRALIAN: Norfolk Island.

>*Lelaps truncatipennis* Dodd 1924: 167-168. Holotype female: Norfolk Island, A.
>
>M. Lea. (SAM, not examined).

turneri Hedqvist. AFROTROPICAL: South Africa, Congo.

>*Dipara turneri* Hedqvist 1969: 193 (Fig. 14). Holotype female: S. Africa, Port
>
>St. John, Pondoland, 6-25 feb., 1924. coll. R. E. Turner. (BMNH, examined). 4
>
>female paratypes: Congo, N. Lae Kivu: Rwankwl, 15.II.1952, coll. J. V. Leroy. (1
>
>female, MRAT, not examined), Kivu: reg. haes Mokoto, Terr. Masisi, VI.1959,

coll. N. Leleup. (1 female, MRAT, not examined), S. Rhodesia: Chipinga, 1200 à

1300 m, VII.1960, coll. N. Leleup. (1 female, KHPC, not examined), S. Africa,

Pondoland, Port St. John, 1-17.III 1924, coll. R. E. Turner. (BMNH, examined).

Dozodipara Desjardins, New Genus

(Fig. 62)

Type Species: *Dozodipara insularis* Desjardins, New Species

Diagnosis: *Dozodipara* is most easily distinguished by a combination of two features.

First, the toruli appear to lie on a shelf, and a sharp angle of 90° separates the upper and

lower face (Fig. 8). The only other diparine genus with this feature is *Conophorisca*.

Second, the propodeum is very steep, being at least as high as long (Fig. 62). While

Cerodipara shares this propodeal shape, it is otherwise unique within Diparinae, all other

genera having propodea at least 1.5X as long as high. *Dozodipara* also has a scutellar

conformation unique within Diparinae: broad, slightly convex, and with the posterior

margin in the same horizontal plane of the body as the anterior margin.

Description: Female. *Head:* Occipital margin rounded; occipital carina present; upper

face without strong, transversely carinate sculpture; eyes not posteriorly extended beyond

occipital margin; inner eye margins uniformly convex; eyes bare; scrobe present and

scrobal channel slightly triangular dorsal to toruli; dorsal margin of scrobe rounded;

toruli on shelf, sharp angle of ~90° between upper and lower face; antennae

symmetrically clavate; antennal formula 11173; pedicel, first funicular segment, second funicular segment subequal in length; claval apex without thick tuft of micropilosity; apical clypeal margin symmetrically bilobed; malar groove present; strong, dark bristles on vertex absent. *Mesosoma:* dorsum of mesosoma without strong, dark bristles; pronotum short, collar-like; notauli strongly arched along entire length (appearing semi-circular) and meeting posterior scutal margin at scutoscutellar suture; lateral lobes of scutum similar in color to remainder of scutum; posterior scutal margin without setose groove; scutellum large, slightly convex with apex near posterior margin, not descending posteriorly; axillae convex , reduced; posterior notal wing process present, pointed; frenum absent; metanotum present as narrow, sculptured band; propodeum at least 1.5X higher than long; propodeum with dorso-ventrally flattened projection near anterior margin; plicae absent; suture between postspiracular area and metapleuron diagonal; propodeal foramen circular, open in one plane; mesepisternal depression absent; prepectus reduced, not reaching tegula; tegula normal, flap-like; subalare not visible; acropleuron slightly convex, partially expanded along dorsal length of mesopleuron; mesopleuron with smooth and sculptured regions posteriorly; metacoxa posteriorly convex, with transverse striations; metacoxa posteriorly without thick vertical brush of setae; 1 metatibial spur, <1.5X width of tibia at point of insertion. *Metasoma:* Petiole cylindrical, without setae, broader than long; GT1 expanded, covering at least half of metasoma length; GT1 rounded lateral to petiole insertion; cercal setae elongate; cercal brush present. **Male:** Unknown.

Discussion: *Dozodipara* is resolved as basal to the clade inclusive of *Conodipara* and *Pyramidophoriella*. This clade is supported by the reduction in the number of metatibial spurs from 2 to 1. This character may be less informative than it seems, however, as some undescribed species of *Conophorisca* and *Myrmicolelaps* were observed to have 2 spurs, suggesting that the character is more homoplastic that it appears to be.

Etymology: *Dozo-* from the bulldozer-like shape of the head (due to the torular shelf) and compact body. *-dipara* to ally the genus with Diparinae.

Number of Species: 1 described.

Distribution: Madagascar.

Hosts: Unknown.

Key to Species: none.

Dozodipara insularis Desjardins, New Species

Type information: Holotype female, CAL: "Madagascar, Toliara, S. Isoky-Vohimena, Forest 730m, 22°41'S 44°50'E, 21.I.1996, Sylvain, B. L. Fisher #1312."

Description: Female. 1.4 mm. *Color:* Brownish orange, with the following exceptions: pedicel+anellus+F1-6, ventral half of GT1-2 brown; forewing with circular brown spot in speculum; posterior margin of GT1, GT2-7 light brown; eyes, scape, legs off-white; F7+clava white; head metallic green. *Head:* subcircular in frontal view, about as wide as high; vertex and face finely areolate; ratio of ocellocular: postocellar: mid-to-lateral

ocellus distance: lateral ocellus diameter about 1.7: 4.2: 1.5: 1; scrobe high, reaching top of midocellus (midocellus in scrobal depression); scrobal basin and walls transversely striate-reticulate; interantennal carina strong but short, reaching about 0.15X height of scrobe; toruli separated by 0.4 torulus diameters; scape height about 1.1X eye height; anellus about 2.5X broader than long; ratio of scape: pedicel: anellus: F1: F2: F3 about 47: 12: 1: 10: 10: 10; F4 and F5 slightly longer than broad; clypeus well delimited.

Mesosoma: Dorsally pronotum transversely striate-reticulate, remainder of mesosoma finely reticulate, reticulations on scutellum in circular pattern; ratio of pronotum: scutum: scutellum: propodeum about 2.3: 2: 2.3: 1; mesosoma dorsally covered in fine, white setae; pronotum 1.7X wider than long; scutellum 2.8X wider than long; marginal rim of scutellum smooth; metanotum narrow band with pits delimited by longitudinal striae; propodeum antero-medially with small, dorso-ventrally flattened projection, with sigmoidal carina emanating from either side; propodeal sculpture dorsal to sigmoidal carina pitted between strong longitudinal carinae, ventral to sigmoidal carina rugose; nucha present as narrow, smooth, raised band; plicae apparently absent, or sigmoidal carinae represent modified plicae; postspiracular sulcus not visible; spiracle 2X own diameter from metanotum; callus covered in fine, white setae, sculpturally present only as posteriorly projecting spike at lateral end of sigmoidal propodeal carina; prepectus triangular and laterally narrow, in similar plane as pronotum; mesepimeron smooth medially and transversely striate along outer margins; femoral depression shallow, transversely striate-rugose, well defined anteriorly and posteriorly; metapleuron smooth anteriorly, rugose posteriorly; coxae bare; meso- and metatibia spinose; metatibial spur about 0.7X width of metatibia at point of spur insertion; metabasitarsus about 3X as long

as wide, 0.4X length of remaining tarsi; hind coxae distinctly transversely striate along posterior margin; wings brachypterous, forewing reduced, widened and squarely truncate distally, about 0.5X length of mesosoma, hindwing reduced and about 0.5 length of forewing. *Metasoma:* About equal in length to mesosoma; ratio of GT1: GT2-6: GT7: ovipositor sheaths 9.7:1:2.5:1; GT1 bare; GT2-3 not visible, GT4 visible only laterally; GT5-6 dorsally with sparse, thin, white setae; GT7 and ovipositor sheath covered in thick, white, setae, except bare spot on GT7 medial to cerci; ovipositor apico-dorsally obscured by sheath. **Male:** Unknown.

Etymology: *insularis*, meaning island, as this specimen was collected on the island of Madagascar.

Distribution: Madagascar.

Hosts: Unknown.

<center>

Lelaps Walker

(Figs. 14-21, 65)

</center>

Lelaps Walker 1843: 47. Type species: *Lelaps pulchricornis* Walker (orig. desig.).

Lelaps Haliday 1844: 299. [Synonomized by Crawford 1912].

Laelaps Agassiz 1846. [Misspelling, noted by Crawford 1912].

Dilaelaps Schulz 1906: 144. [Unnecessary emendation, synonomized by Crawford 1912].

Stenopistha Strand 1910: 26. [Unnecessary emendation, synononimized by Crawford

     1912].

Spalangiolaelaps Girault 1916: 22-23. Type species: *Spalangiolaelaps argenticoxa*

     Girault (orig. desig. and by monotypy). **New synonymy.**

Diagnosis: Within the Diparinae, *Lelaps* is unique in having a median clypeal tooth (Fig.

16). *Lelaps* females also have an F1 which is at least 1.5X longer than F2 (Fig. 14).

Most diparines have an F1 which is subequal in length to F2, although the exception to

this is *Nosodipara ferrana*. However, *Nosodipara ferrana* can be easily distinguished

from *Lelaps* based on the features given the generic entry for *Nosodipara*. Additionally,

Nosodipara's F1:F2 ratio is the result of a reduced F2 rather than an elongate F1.

Discussion: Although the author of *Lelaps* is often cited as either "Walker (1843)" or

"Haliday (1843)", this problem was solved by Crawford (1912). Crawford stated that

although both articles were dated as being published in 1943, a footnote in the journal

with Haliday's description stated that it was actually issued in 1944. Although Walker

referred to a Haliday manuscript in his description of *Lelaps*, he provided a full

description of both the genus and type species in his paper. Crawford properly credited

the generic name to Walker. Additional confusion was generated when *Lelaps* was

misspelled as *Laelaps* by Agassiz (1846), by Walker himself (1862), and by Dalle Torre

(1898). Both Schulz (1906) and Strand (1910) subsequently provided replacement names

for the misspelling, as *Laelaps* was preoccupied. However, since the valid name for the

genus is *Lelaps*, Crawford (1912) synonymized the replacement names.

Lelaps was resolved at the base of the clade containing *Spalangiolaelaps* and *Lelaps noortii* based on the presence of a median clypeal tooth. Additionally, in 1 of 2 most parsimonious reconstructions, an F1 at least 1.5X as long as F2 is also synapomorphic for the clade. Although the clade was only recovered as monophyletic in the preferred analysis, it was always recovered as monophyletic in the preliminary analyses (not shown). *L. noortii*'s relationship with the remainder of *Lelaps* is discussed in the former's specific entry.

Heydon and Boucek (1992) discussed the potential synonymy of *Spalangiolaelaps* with *Lelaps sensu stricto*, although they maintained it as a valid genus, as the male was unknown at the time. However, the male of *Spalangiolaelaps* was identified during this study and resembles the male of *Lelaps sensu stricto* in all phylogenetic and diagnostic characters. The female of *Spalangiolaelaps* has been historically separated from *Lelaps* based on the following characters: absence of wings, absence of frenum, mandible with 4 teeth, nucha long and tapering posteriorly, and notauli reaching scuto-scutellar margin without joining. Examination of many described species of *Lelaps sensu stricto* have shown the last 3 of these characters to be variable within the genus. In fact, the majority of Neotropical *Lelaps sensu stricto* have notauli that do not join before reaching the scuto-scutellar margin. As many diparine genera have species with both macropterous and brachypterous forms (e.g. *Dipara*), and this is generally considered a very plastic character within the subfamily, the only remaining character separating the two entities is the presence/absence of the frenum. Examination of four undescribed brachypterous species in the *Lelaps*/*Spalangiolaelaps* clade has shown variation in this feature. One undescribed species from the United States (Arizona

and Florida, CNC) does have a frenum, but resembles *Spalangiolaelaps* in all other defining characters. The other three species (two from Cuba and one from the Dominican Republic, CNC) lack the frenum, but differ from *Spalangiolaelaps* in other features. These additional taxa were not included in the phylogenetic analysis because of the already strong support for the inclusion of *Spalangiolaelaps* in *Lelaps* and the desire to keep the number of taxa in the morphological analysis limited (i.e., to maintain a character:taxon ration as high as possible). However, in retrospect the inclusion of these taxa may have helped elucidate the relationships of *Lelaps sensu stricto*, *Spalangiolaelaps*, and *Noortia* in the broader context of diparine phylogeny. Regardless, due to the similar morphology of the males and the presence of variability of all characters used to separate the two genera within *Lelaps sensu stricto*, the genus *Spalangiolaelaps* is herein synonomized with *Lelaps*.

Number of Species: 42 described species, possibly hundreds of undescribed species.

Distribution: New World.

Hosts: One species was reared from a boll weevil relative (Curculionidae, J. Woolley, pers. com.).

Key to Species: Yoshimoto (1977) provided a key to the Nearctic species. Although a key to the world species is not given here, characters used to separate *Lelaps noortii* from the remainder of *Lelaps* are given in the *L. noortii* diagnosis.

Species of *Lelaps*:

abdominalis Ashmead. NEOTROPICAL: Brazil.

Lelaps abdominalis Ashmead 1904: 481-482 (Plate 36, Fig. 1). Holotype female:

Brazil: P. Branca, in April. (USNM, examined).

aeneiceps Ashmead. NEOTROPICAL: Brazil.

Lelaps aeneiceps Ashmead 1904: 481. Type information uncertain: Brazil:

Chapada and Santarem. (USNM, examined).

affinis Ashmead. NEOTROPICAL: Brazil.

Lelaps affinis Ashmead 1904: 480. Holotype female: Brazil: Santarem. (USNM,

examined).

albipes Cameron. NEOTROPICAL: Panama.

Lelaps albipes Cameron 1884: 132. Holotype female: Panama. (BMNH,

examined).

albofasciatus Hedqvist. NEOTROPICAL: Puerto Rico?.

Lelaps albofasciatus Hedqvist 1964: 57-58 (Fig. 6). Holotype female: "Portorico,

Moritz, L. nr. 15181." (ZMHB, not examined).

annulicornua (Strand). NEOTROPICAL: Peru.

Stenopistha annulicornua Strand 1911: 200. Holotype female: Peru, Pachitea River.

apicalis Ashmead.   NEOTROPICAL: Brazil.

Lelaps apicalis Ashmead 1904: 479-480. Holotype female: Brazil: Chapada, in August. (USNM, not examined).

argenticoxa (Girault). NEARCTIC: USA (Maryland).

Spalangiolaelaps argenticoxa Girault 1916: 23. Holotype female: MD: Prince George's County, Hillmead (Glenndale), forest, sweeping, June 4, 1916. (USNM, not examined). New synonymy.

avicula Haliday.

Lelaps avicula Haliday, 1844: 300. (Type gender and locality uncertain).

beckeri Yoshimoto. NEARCTIC: Canada, USA (Missouri).

Lelaps beckeri Yoshimoto 1977: 1052-1054 (Figs. 5, 13, 14, 24, 30). Holotype female: MO: Williamsville, VII-IX.69, coll. J. T. Becker, malaise trap. Allotype male: MO: Williamsville, 12-26.V.1969, coll. J. T. Becker, malaise trap. 1 female and 7 male paratypes: Ontario: Stittsville, 19.VIII.68, coll J. R. Vockeroth (1 female), Ontario: Rondeau Prov. Park, 8-12.VIII.73, malaise trap (3 males), Ontario: Rondeau Prov. Park, 19.VI.62, 10.VII.62, coll. S. M. Clark (2 males),

Ontario: Crow Lake, Marmora area, 18.VIII.59, coll. L. K. Smith (1 male),

Quebec: Meach Lake, 8.IV.62, coll. S. M. Clark (1 male). (CNC, not examined).

bimaculata Ashmead. NEOTROPICAL: Brazil.

Lelaps bimaculata Ashmead 1904: 482. Type information uncertain: Brazil:

Chapada, in April; Santarem; and P. Branea. (USNM, not examined).

callisto Marshall. NEOTROPICAL: Venezuala.

Laelaps callisto Marshall 1892: 73. Holotype female: Venezuala. [De Santis

1979: 121 is the earliest listing of this species as *Lelaps callisto*. However, no

mention is made of the misspelling.]

caudatula (Strand). NEOTROPICAL: Peru.

Stenopistha caudatula Strand 1911: 201-202. Holotype female: Peru, Pachitea

River.

decorata Walker. NEOTROPICAL: Brazil.

Laelaps decorata Walker 1862: 390. Holotype female: Ega. (BMNH, examined)

[De Santis 1980: 226 is the earliest listing of this species as Lelaps decorata.

However, no mention is made of the misspelling.]

ferrierei Hedqvist. NEOTROPICAL: Brazil.

Lelaps ferrierei Hedqvist 1964: 56-57 (Fig. 5). Holotype female: Brazil, Nova Teutonia (27°11' B 52°23' L), June 1, 1945, coll. F. Plaumann. (KHPC, not examined).

ferruginea Cameron. NEOTROPICAL: Panama.

Lelaps ferruginea Cameron 1884: 133. Holotype female: Panama. (BMNH, examined).

flagellata (Strand). NEOTROPICAL: Bolivia.

Stenopistha flagellata Strand 1911: 208-209. Holotype female: Eastern Bolivia (Steinbach).

flavescens Ashmead. NEOTROPICAL: St. Vincent, Grenada.

Lelaps flavescens Ashmead 1894: 156-157. 2 females and 3 males (designation uncertain, although 1 of the females is likely the holotype): St. Vincent. (USNM, not examined).

floridensis Yoshimoto. NEARCTIC: USA (Florida), NEOTROPICAL: Virgin Islands.

Lelaps floridensis Yoshimoto 1977: 1048-1052 (Figs. 4, 11, 12, 23, 29). Holotype female and allotype male: Miamai, FL, 17.VI.49, coll. C. D. Link, in trap, S.P.B. Acc. No. 103433. (FSCA, not examined). 8 female and 1 male paratypes: FL: Miami, 4.III.49, coll. C. D. Link, in trap, S.P.B. Acc. No. 103614 (1 female, FSCA, not examined), FL: Coral gables, 25.III.49, coll. C. D. Link,

S.P.B. Acc. No. 103990. (1 female, FSCA, not examined), FL: Matheson

Hammock, Dade Co., 26.V.62, coll. R. E. Woodruff (2 females, FSCA, not

examined), FL: Matheson Hammock, 13.II.57, coll. J. Porter, on *Celtis laevegata*

(1 female and 1 male, FSCA, not examined), FL: Ross and Castellow Hammock,

Dade Co., 12.IV.72, coll. H. V. Weems, Jr. (1 female, FSCA, not examined), FL:

Paradise Key, 7.IV.51, coll. H. and M. Townes. (1 female, AEI, not examined),

Virgin Islands: St. Croix, airport, 6.IV.68, coll. W. H. Pierce, sweeping. (1

female, FSCA, not examined).

halidayi Ashmead. NEOTROPICAL: Brazil.

> *Lelaps halidayi* Ashmead 1904: 481. Holotype female: Brazil: Rio de Janeiro, in
>
> October. (USNM, examined).

> *Stenopistha halidayi sobrina* Strand 1911: 199. Holotype female: Brazil: Rio de
>
> Janeiro (v. Olfers). [Subspecies]

insularis Mercet. NEOTROPICAL: Santa Isabel.

> *Lelaps insularis* Mercet 1927: 57-60. Holotype female: Isla de Fernando Poo:
>
> Santa Isabel. (type location uncertain).

magnifica (Strand). NEOTROPICAL: Colombia.

> *Stenopistha magnifica* Strand 1911: 204-205. Holotype female: Bogota (Lindig).

melinus Yoshimoto. NEARCTIC: USA (Lousiana, Maryland, South Carolina, Tennessee).

Lelaps melinus Yoshimoto 1977: 1054-1055 (Figs. 15, 31). Holotype male: LA: Bayou Chicot, Evangeline Parish, 11-14.VIII.71, coll D. Shanek. (CNC, not examined). 3 male paratypes: MD: Takoma Park, 12.VIII.73, coll. H. and M. Townes. (1 male, AEI, not examined), SC: Anerson, 21.VII.57, coll. J. G. Chillcott. (1 male, CNC, not examined), TN: Lexington, Natchez Trace State Park, 20-26.VI.72, coll. G. Heinrich, malaise trap. (1 male, CNC, not examined).

ornata (Strand). NEOTROPICAL: Peru.

Stenopistha ornata Strand 1911: 206. 2 females (designation uncertain): Caracas (Moritz).

paraguayensis Girault. NEOTROPICAL: Paraguay.

Lelaps paraguayensis Girault 1912: 170-171. Holotype female: Paraguay, San Bernadino, coll. K. Fiebrig. (Zool. Mus. Berlin, not examined)

picta Walker. NEOTROPICAL: Brazil.

Laelaps picta Walker 1862: 390. Holotype female: Ega. [Boucek and Delvare 1992 designated a Lectotype female (BMNH, examined)].

pulchella (Strand). NEOTROPICAL: Venezuala.

Stenopistha pulchella Strand 1911: 203. Holotype female: Caracas (Mortiz).

pulchra Girault. NEOTROPICAL: Paraguay.

> *Lelaps pulchra* Girault 1912: 171-172. Holotype female: Paraguay, San
> Bernadino, coll. K. Fiebrig. (Zool. Mus. Berlin, not examined)

pulchricornis Walker. NEOTROPICAL: St. Vincent.

> *Lelaps pulchricornis* Walker 1843: 47. Holotype female: St. Vincent. (BMNH,
> not examined).

pygata (Strand). NEOTROPICAL: Peru.

> *Stenopistha pygata* Strand 1911: 202. Holotype female: Peru, Pachitea River.

> *Stenopistha pygata conjuncta* Strand 1911: 202-203. Holotype female: Peru,
> Pachitea River. [Subspecies]

rectivitta (Strand). Neotropical: Peru.

> *Stenopistha rectivitta* Strand 1911: 206-207. 2 females (designation uncertain):
> Peru, Pachitea River.

rhomboidea (Strand). NEOTROPICAL: Colombia.

> *Stenopistha rhomboidea* Strand 1911: 205-206. Holotype female: Bogota
> (Lindig).

sadales (Walker). NEOTROPICAL: Galapagos.

> *Merostenus sadales* Walker 1839: 93. Holotype female: Charles' Isle, Galapagos.
> (BMNH, not examined).

setifrons (Strand). NEOTROPICAL: Peru.

> *Stenopistha setifrons* Strand 1911: 207-208. Holotype female: Peru, Pachitea
> River.

simplex (Fabricius). NEOTROPICAL: Guyana.

> *Chalcis simplex* Fabricius 1804: 164. [Boucek and Delvare (1992) designated a
> female lectotype (Guyana, ZMUC, not examined) and transferred the species to
> *Lelaps*.]

striaticeps (Strand). NEOTROPICAL: Peru.

> *Stenopistha striaticeps* Strand 1911: 208. Holotype female: Peru, Pachitea River.

striatus Yoshimoto. NEARCTIC: USA (Missouri, Georgia, Texas).

> *Lelaps striatus* Yoshimoto 1977: 1055 (Figs. 6, 7, 16-18, 32-34). Holotype male:
> MO: Williamsville, 29.VI.-5.VII.69, coll. J. T. Becker, malaise trap. 28 male
> paratypes: MO: Williamsville, 29.VI-5.VII.69, 16-26.VI.69, 26.V-16.VI.69, 17-
> 29.V.70, coll. J. T. Becker, malaise trap (16 males), GA: 5.V-14.V.71, 5-
> 10.VI.71, 28.V-9.VI.70, 25.VIII.70, coll. F. T. Naumann, malaise trap (7 males),
> GA: Forsyth, 20-21.V.70, coll. G. Heinrich (2 males), GA: Holcomb Creek,

1.VIII.57, coll. W. R. Richards (1 male), TX: Welder Wildlife, Ref. nr. Sinton,

23.III.65, coll. J. G. Chillcott (2 males). (CNC, not examined).

stylata Ashmead. NEOTROPICAL: Brazil.

Lelaps stylata Ashmead 1904: 482. Type information uncertain: Brazil: Chapada,

in April; Santarem. (USNM, not examined).

tapajoana (Schulz). NEOTROPICAL: Brazil.

Dilaelaps tapajoana Schulz 1906. [Replacement name for *Lelaps ferruginea*

Ashmead 1904, preoccupied by *Dilaelaps ferruginea* Cameron 1884.]

Lelaps ferrunginea Ashmead 1904: 480. Holotype female: Brazil: Santarem.

terebrans (Strand). NEOTROPICAL: Peru.

Stenopistha terebrans Strand 1911: 200-201. Holotype female: Peru, Pachitea

River.

viridiceps (Strand). NEOTROPICAL: Peru.

Stenopistha viridiceps Strand 1911: 199-200. Holotype female: Peru, Pachitea

River.

vittipennis (Strand). NEOTROPICAL: Peru

Stenopistha vittipennis Strand 1911: 203-204. Holotype female: Peru, Pachitea

River.

Lelaps noortii Desjardins, New Species

(Fig. 65)

Type information: Holotype female (SAM): "South Africa, W. Cape, Koeberg Nature

Reserve, 33°37.62'S 18°24.26'E, 27 Dec 1997-23 Jan 1998, S. van Noort, KO97-Y158,

Yellow Pan Trap (cup), Station 5, West Coast Strandveld dominated by *Euphorbia* and

Rhus spp." 1 paratype female (SAM): same data as holotype except "31 Oct – 28 Nov

1997, KO97-Y111, Yellow Pan Trap (bowl), Station 3."

Diagnosis: *Lelaps noortii* can be distinguished from the remaining species of *Lelaps* by

its posteriorly smooth metacoxa, absence of bristles, and filiform antennae. The

remainder of *Lelaps* have transverse striations on the posterior margin of the metacoxa,

strong, dark bristles on the vertex and dorsal surface of the mesosoma, and clavate

antennae.

Description: Female. 1.9 mm. *Color:* Brownish black with metallic green and blue

highlights, with the following exceptions: Scape, pedicel brownish orange, flagellum

brown, eyes grey, scutellum metallic yellowish green, propodeum mostly metallic

greenish blue, nucha metallic bluish green, all legs yellowish white to brownish orange,

ovipositor yellowish orange. *Head:* Circular in frontal view, 0.9X as high as wide; eye

sparsely setose, 1.4X as high as wide; vertex smooth, remaining head longitudinally strigose (Eady); ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 4.3:6.3:4:1; scrobe high, narrow, reaching to 0.8X distance to mid-ocellus; scrobal basin and walls coriaceous-imbricate; interantennal carina absent; toruli separated by 0.6X torulus diameters; scape height about 0.9X eye height; anellus about 3X broader than long; ratio of scape: pedicel: anellus: F1: F2: F3 about 35: 12: 1: 15: 9: 9; F4 and F5 about 1.5X as long as broad; clypeal boundaries indistinct. *Mesosoma:* Dorsally pronotum finely, transversely strigose (Eady), scutum medial to notauli and axillae finely alveolate, scutum lateral to notauli smooth, scutellum longitudinally strigose (Eady); ratio of pronotum: scutum: scutellum: propodeum about 1.2: 1.4: 1.4: 1; mesosoma bare except scutum dorsally with sparse, fine, white setae; pronotum 2.3X wider than long; scutum 2.3X wider than long; marginal rim of scutellum with lightly grooved, pitted lamella; metanotum narrow band with pits delimited by longitudinal striae; propodeum along anterior margin with pits delimited by longitudinal carinae, remainder of propodeum areolate, becoming more irregular lateral to plica; nucha indistinct; plica present as longitudinal carina; postspiracular sulcus smooth with pits delimited by transverse carinae; spiracle small, 3.5X own diameter from metanotum; callus mostly bare except for a few fine, white setae, projecting posteriorly as point beyond postspiracular sulcus; prepectus triangular, in similar plane as pronotum, abutting at about 160° angle; mesepimeron mostly smooth, with dorsal and ventro-posterior margins pitted; femoral depression shallow, areolate, well defined anteriorly and posteriorly; metapleuron smooth; coxae anteriorly with few fine, white setae; meso- and metatibia spinose; longer metatibial spur about 1.7X length of shorter, 0.6X width of

metatibia at point of spur insertion; metabasitarsus about 3.8X as long as wide, 0.6X length of remaining tarsi; hind coxae faintly transversely striate along posterior margin; wings brachypterous, forewing reduced, pointed antero-distally, about 0.7X length of mesosoma, hindwing reduced, about 0.6 length of forewing, with fringe-like setae on distal margin. *Metasoma:* About 1.9X length of mesosoma; ratio of GT1: GT2-6: GT7: ovipositor sheaths 5:1:1.5:1.5; GT1-4 bare; lateral surface of GT5, all of GT6-7 and ovipositor sheath covered in fine, white, setae; ovipositor apico-dorsally smooth. **Male:** Unknown.

Discussion: In preliminary phylogenetic analyses (not shown), *Lelaps noortii* was always placed a sister-group to the *Lelaps* + *Spalangiolelaps* clade. However, in the final phylogenetic analysis *L. noortii* is nested within the *Lelaps* clade as sister-taxon to *Spalangiolaelaps*. This relationship is based on 2 synapomorphies (loss of the frenum and strongly arched, closely spaced notauli), both of which are highly homoplastic in the analysis. The loss and gain of the frenum may be even more plastic than suggested by this analysis; this possibility is discussed in *Lelaps*' generic entry. However, it should also be noted that *L. noortii* has metallic coloration over most of it's body. While this trait was not coded in the phylogenetic analysis, it is generally rare throughout Diparinae although common in *Lelaps*.

Within the *Lelaps* clade, *L. noortii* has 5 autapomorphic features: posteriorly smooth metacoxa, absence of bristles, filiform antennae, an elongate pedicel which is subequal in length to F1, and absence of a malar groove. None of these traits are unique to *L. noortii* within Diparinae and all could become sympleiso- or synapomorphic given

an alternate placement of the taxon. Also, *L. noortii* and the remainder of *Lelaps* have extremely disjunct distributions. *L. noortii* is found only the Western Cape Province of South Africa, while *Lelaps* is endemic to the New World. *L. noortii* may be a relict of a time when *Lelaps* had a broader range across a combined South America and Africa, or it may represent a recolonization of Africa from South America. Although *L. noortii* may represent the sister-taxon to the remainder of *Lelaps* and therefore be recognizable as a genus, the results of the final phylogenetic analysis warrant the description of *L. noortii* as a species of *Lelaps*. However, a species-level phylogenetic study of *Lelaps* itself may be needed to ascertain the true relationship between the two taxa.

Etymology: Named for Simon van Noort of the Cape Town Museum (South Africa), who provided much new African material which was vital for this study, and who assisted in my collection of diparines during my visit to Cape Town.

Distribution: South Africa, Western Cape.

Hosts: Unknown.

Myrmicolelaps Hedqvist

(Figs. 25-35, 63, 64)

Myrmicolelaps Hedqvist 1969: 182. Type species: *Myrmicolelaps paradoxus* Hedqvist

 (orig. desig. and by monotypy).

Dolichodipara Hedqvist 1969: 180-181. Type species: *Dolichodipara scutellata*

Hedqvist (orig. desig. and by monotypy). **New synonymy.** [Type specimen of

genus examined]

Diagnosis: *Myrmicolelaps* belongs to a clade with *Conophorisca*. This entire clade can

be diagnosed with 2 characters: 1) propodeal foramen hinge-like, open both dorsally and

ventrally (Fig. 31). All remaining diparines have a propodeal foramen that is circular and

open only in 1 plane. 2) Petiole constricted antero-ventrally (Fig. 34). All other

diparines have a cylindrical petiole, or in the case of *Conodipara*, an L-shaped petiole.

Myrmicolelaps can be distinguished from *Conophorisca* by the following characters.

First, in *Myrmicolelaps* the axillary wing sclerite is expanded and visible (Fig. 30), while

it is neither expanded nor visible in *Conophorisca*. Second, *Conophorisca* has its toruli

located on a shelf, where the upper face is separated from the lower face by a sharp angle

of ~90° (Fig. 8), while no sharp 90° angle is present in *Myrmicolelaps*.

Discussion: Hedqvist (1969a) separated these *Myrmicolelaps* from *Dolichopdiara* based

on scutellum shape. *Dolichodipara* has a moderately tooth-like scutellum, while

Myrmicolelaps has a flat scutellum. However, *Myrmicolelaps aurantius* has a the

posterior portion of its scutellum slightly raised, and this character shows a grade of

variability throughout both described and undescribed species. The *Myrmicolelaps* clade

is supported as monophyletic in the phylogenetic analysis by 2 synapomorphies: the

presence of an expanded axillary wing sclerite and presence of a grooved, setose

posterior scutal margin. Based on the strong synapomorphies uniting this clade, and the

variability that exists within characters traditionally used to divide it, *Dolichodipara* Hedqvist is herein synonomized with *Myrmicolelaps* Hedqvist. As both genera are described in the same paper, the name *Myrmicolelaps* is chosen for 2 reasons. First, the name itself provides more information about the taxon, hinting at the genus' ant-like appearance. Second, *Myrmicolelaps* is more commonly recognized by chalcidologists, and is present in many more collections than *Dolichodipara*.

Very few host records exist for the diparines in general. However, a single specimen of *Myrmicolelaps* from Zimbabwe (S. Rhodesia), representing an undescribed species (*Dolichopdipara* Heqvist clade), was found in the USNM collection pinned above a tsetse fly (Glossinidae: *Glossina*) puparium with an exit hole and host tissue inside. The specimen label reads "S. Rhodesia, Kariba, 4/X/1965, R. J. Phelps", and a smaller label beneath reads only "745." Previously, within Chalcidoidea only eupelmids (*Eupelminus tarsatus*, *Anastus viridiceps*, *Anastatus sp.*) and chalcidids (*Dirhinus inflexus*, *Chalcis amenocles*) were known to parasitize tsetse puparia (Leak 1999). Additionally, another undescribed species (*Myrmicolelaps* Hedqvist clade) from South Africa (Orange Free State) was reared from mantid egg cases (Prinsloo pers. comm.).

Species/Distribution: 6-7 sp. (3 described) South Africa, Western Cape; 2-3 sp. (1 described), Namibia; 1 undescribed sp. South Africa, Mpumalanga, 1 undescribed sp. Zimbabwe.

Hosts: An undescribed species from Zimbabwe was reared from a tsetse fly (Glossinidae: *Glossina*) puparium, and another undescribed species was reared from a mantid egg case.

Key to Species: Given below.

Key to species of *Myrmicolelaps* Hedqvist

1.   Metanotum present as large, vertical, smooth, shiny surface; propodeum rising

   posteriorly in lateral view; occipital carina distinct   2

   Metanotum not visible; propodeum level or descending posteriorly in lateral

   view; occipital carina indistinct   3

2.   Clypeal margin sinuate; lateral surface of pronotum with deep, rounded,

   longitudinal depression delimited by carina both dorsally and ventrally

                                                                     Myrmicolelaps scutellata

                                                                     Hedqvist

   Clypeal margin with 2 strong teeth; lateral surface of pronotum without deep,

   rounded, longitudinal depression delimited by carina both dorsally and ventrally

                                                                     Myrmicolelaps iridius

                                                                     Desjardins, new species

3.   Pronotum conical; occipital margin carinate; propodeum with distinct suture

   separating nucha from rest of propodeum   *Myrmicolelaps paradoxus*

                                                                     Hedqvist

   Prontum slightly bulging laterally and dorsally; occipital margin rounded;

   propodeum without suture separating nucha from rest of propodeum

                                                                     Mymricolelaps aurantius

                                                                     Desjardins, new species

Species of *Myrmicolelaps*:

paradoxus Hedqvist. AFROTROPICAL: South Africa.

> *Myrmiolelaps paradoxus* Hedqvist 1969: 182-183. Holotype female: S. Africa, Orange F. State, Harrismith, March 1-20, 1927, coll. R. E. Turner. (BMNH, examined). Paratype male: S. Africa, Cape Prov., Aliwal North, Dec. 1922, coll. R. E. Turner. (BMNH, examined).

scutellata (Hedqvist). AFROTROPICAL: South Africa.

> *Dolichodipara scutellata* Hedqvist 1969: 181-182. Holotype female: S. W. Africa, Aus. 8-30.XI, 1929, coll. R. E. Turner. (BMNH, examined). Paratype female: S. W. Africa, Aus. Dec. 1929, coll. R. E. Turner. (KHPC, not examined).

*Myrmicolelaps iridius***, New Species**

(Fig. 63)

Type Information: Holotype female (SAM). "Namibia, Waterberg area, Kleinwater Farm, on sand, C. Dickman. Collected April 1992, ex. pitfall trap, voucher specimen for job no. 1992/006. SAM-HYM P008338." 1 paratype male (SAM), same data as female except "SAM-HYM P008339."

Description: Female. 3.5 mm. *Color:* Dark brown with the following exceptions: Head mostly metallic green with metallic blue in scrobal basin and along posterior eye margin, clypeus gold dorsally to reddish gold ventrally, distal 3/4 of scape brownish yellow, latero-ventral margin of pronotum white, scutellum reddish gold, all coxae, mesepisternum, and mesepimeron brownish green with metallic blue highlights posteriorly, propodeum and petiole mostly metallic greenish-brown, nucha brownish yellow, all tibiae brown, lightening to brownish yellow distally, all tarsi 1-3 brownish yellow, all tarsi 4-5 brown, gastral sternites and ovipositor sheaths brown. *Head:* Subtriangular-ovate in frontal view, 1.2X as high as wide; eyes sparsely setose, 1.8X as high as wide; head mostly coriaceous-imbricate, genae longitudinally strigose (Eady); raised, rounded transverse ridge present between lateral ocelli, causing ocelli to face latero-dorsally; ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 1.8:4.2:1.7:1; scrobe high, narrow, reaching from torulus to dorsal margin of mid-ocellus (mid-ocellus in scrobe); scrobal basin smooth, scrobal walls smooth to coriaceous; margin of scrobal walls rounded dorsally and strongly carinate ventrally; interantennal carina raised, flattened, reaching 0.3X height of scrobe; toruli separated by 1.5 torulus diameters; scape length 1.3X eye height; ventral surface of scape rounded; scape straight dorsally, bulging and bowed inward ventrally; anellus reduced and partially fused to F1; ratio of scape: pedicel: anellus+F1: F2: F3 about 5.2:1:2:1.8:1.6, F4 5.8X as long as wide to F7 2.8X as long as wide; clava fused, 1-segmented; malar sulcus indistinct, although faint longitudinal depression present; gena rounded posteriorly; clypeus strongly delimited laterally, indistinct dorsally; clypeal margin protruding with 2 strong teeth. *Mesosoma:* Dorsally coriaceous, except metanotum which is smooth,

polished; dorsally with sparse, white setae (slightly more dense on scutellum); ratio of

pronotum: scutum: scutellum: propodeum about 3.3:1:1.2:2.7; pronotum about as wide as

long (although partially obscured dorsally by mounting); lateral surface of pronotum with

deep, rounded, longitudinal depression delimited by carina both dorsally and ventrally;

scutum >2X as wide as long (partially obscured dorsally by mounting); posterior scutellar

margin smooth; metanotum wide, transverse, vertical band; propodeum antero-medially

coriaceous, antero-laterally transversely striate, becoming longitudinally striate

posteriorly; plicae absent; postspiracular sulcus wide, shallow, mostly smooth; spiracle

2X its own diameter from metanotum; spiracle facing postero-laterally; prepectus

triangular, in same plane as pronotum; acropleuron smooth ventrally to coriaceous

medially to diagonally striate antero-laterally; mesepisternum antero-ventrally areolate,

postero-dorsally transversely striate, mesepimeron anteriorly areolate-transversely striate,

posteriorly smooth, except dorso-posteriorly coriaceous; femoral depression distinct

dorsally, less distinct posteriorly, indistinct anteriorly; metapleuron areolate, with large,

irregular transverse striae near coxal insertion; metapleuron fused to propodeum anterior

to propodeal spiracle; 1 metatibial spur, 1.5X width of metatibia at point of insertion;

metabasitarsus about 6.7X as long as wide, about 0.5X length of remaining tarsi;

posterior 1/2 of metacoxa transversely striate; pro- and mesocoxa anteriorly with sparse,

white setae; meso- and metatibia not spinose; apterous, forewing reduced to membranous

lump anteriorly, hindwing apparently absent. *Metasoma:* 1.4X length of mesosoma;

petiole about 2.3X as long as broad, transversely striate ventrally, rough-areolate

laterally, imbricate dorsally; ratio of GT1: GT2-6: GT7: ovipositor sheaths about

4.5:3.9:1:1; all tergites dorsally covered in white setae (separated by 0.5-1X setal length),

except sparse to absent in anterior 4/5 of GT1 and anterior 2/3 of GT5, and dense on GT6-7 and ovipositor sheaths; ovipositor tip apico-dorsally serrate. **Male:** Same as female.

Etymology: from *irido-*, meaning rainbow, from the variety of colors present on the specimen.

Distribution: Namibia.

Hosts: Unknown.

Myrmicolelaps aurantius, New Species

(Figs. 25-35, 64)

Type Information: Holotype female (CNC). "S.A.E. Trans. Guernsey Farm, 15km.E.Klaserie, XII-19-31-1985, yellow mal., M. Sanborne." Paratypes: 5 females and 5 males, same data as holotype.

Description: Female. 2.3 mm. *Color:* Bright orange with the following exceptions: head metallic green; antenna - clava brownish yellow, clava light brown; mesepimeron ventral to acropleuron, posterior margin of metacoxa brownish with metallic purple; mesocoxa brown dorsally to off-white ventrally; legs mostly whitish orange, with distal end of metatibia brown; gaster brownish orange, with bronze highlights developing posteriorly; ovipositor sheath brown. *Head:* Ovate in frontal view, about as high as wide; eyes sparsely setose, *1.9X as high as wide*; head mostly finely areolate; lateral ocelli not on

raised, rounded transverse ridge, facing slightly laterally, mostly dorsally; ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 2.3:4.9:2:1; scrobe high, narrow, reaching from torulus to dorsal margin of mid-ocellus (mid-ocellus in scrobe); scrobal basin and walls finely areolate; interantennal area carinate, not flattened, reaching 0.3X height of scrobe; toruli separated by 1.6 torulus diameters; scape length subequal to eye height; ventral surface of scape rounded; scape slightly laterally bowed inward; anellus reduced and partially fused to F1; ratio of scape: pedicel: anellus+F1: F2: F3 about 4:1:1.3:1.1:1.2, F4 2.5X as long as wide to F7 2.2X as long as wide; clava fused, 1-segmented; malar sulcus distinct; clypeus strongly delimited laterally, indistinct dorsally; clypeal margin protruding and with 2 symmetrical rounded lobes. *Mesosoma:* Dorsally mostly very finely areolate, except scutum smoother medial to notauli; dorsally with sparse, white setae; ratio of pronotum: scutum: scutellum: propodeum about 3.1:1:1.1:3.7; pronotum about 1.1X longer than wide; pronotum without lateral depression; scutum 2.1X as wide as long; posterior scutellar margin smooth; metanotum narrow band, sculpturally undifferentiated from propodeum; propodeum anteriorly finely areolate, becoming longitudinally strigose (Eady) posteriorly; plicae absent; postspiracular sulcus wide, shallow, mostly smooth; spiracle 6X its own diameter from metanotum; spiracle facing postero-laterally; prepectus triangular, in same plane as pronotum; acropleuron coriaceous ventrally to finely areolate dorsally; mesepimeron areolate; femoral depression indistinct; metapleuron finely areolate; metapleuron distinct from propodeum anterior to propodeum spiracle; 1 metatibial spur, 1.1X width of metatibia at point of insertion; metabasitarsus about 7.2X as long as wide, about 0.6X length of remaining tarsi; posterior 1/2 of metacoxa

transversely striate; pro- and mesocoxa anteriorly mostly bare; mesotibia with single spine on inner surface; metatibia not spinose; apterous, forewing and hindwing apparently absent. *Metasoma:* 1.2X length of mesosoma; petiole about 2.2X as long as broad, mostly finely areolate except transversely striate antero-ventrally; ratio of GT1: GT2-6: GT7: ovipositor sheaths about 7:2:1.8:1; GT1-7, ovipositor sheath with white setae; ovipositor tip apico-dorsally serrate. **Male:** Same as female.

Etymology: from *auranti-*, meaning orange, from the bright orange coloration on the meso- and meta-soma of the specimen.

Distribution: South Africa, Eastern Transvaal.

Hosts: Unknown.

Neapterolelaps Girault

(Figs. 36-41, 50, 51, 56, 57)

Neapterolelaps Girault 1913[175]: 86-87. Type species: *Neapterolelaps lodgei* Girault (orig. desig. and by monotypy).

Australolaelaps Girault 1925: 96. Type species: *Australolaelaps aeniceps* Girault (by monotypy). **New synonymy.** [Type specimen of genus examined]

Austrolaelaps Girault 1929: 2. Type species: *Austrolaelaps nigrisaepta* Girault (by monotypy). [Synonomized by Boucek 1988]

Pinocchio Pagliano & Scaramozzino 1990. [Unneccesary emendation, synonymized by Noyes 2003]

Diagnosis: *Neapterolelaps* can be identified by 3 unique features: 1) metacoxa posteriorly with vertical brush of white setae (Fig. 39), 2) anterior surface of GT1 lateral to petiole with thick tufts of white setae (Fig. 37, 38), 3) longer metatibial spur at least 2X width of the metatibia at point of insertion (Fig. 40). Additionally, all species of *Neapterolelaps* have a carinate posterior genal margin, a carinate occipital margin, sparsely setose eyes, and lack both the typical diparine bristles and a frenum.

Discussion: Boucek (1998) synonomized *Austrolaelaps*, based on the fact that the only difference between the females of the two genera was propodeal sculpture variation, and no differences between the males existed. Pagliano and Scaramozzino (1990) offered the replacement name *Pinocchio*, as they incorrectly claimed *Neapterolelaps* was preoccupied. Noyes (2003) states that it was offered as a replacement name for *Neapterolelaps* Dodd, although it was obvious Pagliano and Scaramozzino meant *Neapterolelaps* Girault.

Two new species of *Neapterolelaps* are described here, *viridescens* and *mitteri*, which bridge the morphological gap between the genera *Australolaelaps* Girault and *Neapterolaelaps* Girault. *N. viridescens* and *N. mitteri* possess notauli, a scutellum, and a prepectus similar to *Australolaelaps* Girault, while their antennae and epipygium resemble that of *Neapterolelaps* Girault. *N. viridescens and N. mitteri* have only one feature which are unique among the clade: they are brachypterous, having wings intermediate in size between the two genera. This character was not coded in the phylogenetic analysis, because it is extremely variable within many taxa. Additionally,

N. viridescens has a slightly more clavate antenna and longer wings than *N. mitteri* (both characters have been historically used to distinguish *Australolaelaps* Girault from *Neapterolelaps* Girault), suggesting that these taxa may be snapshots into a spectrum of continuous variation.

The new species have distribution disjunctive from both *Australolaelaps* Girault and *Neapterolaelaps* Girault (*N. viridescens* and *N. mitteri* are found in southeastern Australia and Tasmania, while *Australolaelaps* Girault and *Neapterolelaps* Girault are found in Northeastern Australia and surrounding islands). Perhaps *N. viridescens* and *N. mitteri* represent relict species left from a time when the entire clade had a much wider distribution, and a variety of intermediate forms existed. As the two newly described species would likely form a paraphyletic taxon if described as new genus, *Australolaelaps* Girault is herein synonymized with *Neapterolelaps* Girault despite the large suite of morphological features separating the two taxa.

Neapterolelaps is sister-group to the remainder of Diparinae and represents the only lineage of diparines to evolve before the typical pattern of bristles so often used to identify the subfamily. Molecular results (Desjardins et al., in prep) showed strong groupings of *Neapterolelaps* and the remainder of Diparinae. However, the molecular data had significant difficulty in uniting these groups, supporting the hypothesis that this is an ancient split within Diparinae. Morphologically, *Neapterolelaps* is defined by 3 non-homoplastic and 4 homoplastic synapomorphies as discussed in the diagnosis.

Number of Species: 6 described species, many undescribed (>10).

Distribution: Eastern Australia: north to Papua New Guinea, east to New Caledonia, and south to Tasmania. Collected in forested areas, particularly rainforests. Boucek (1988) mentioned an undescribed species near *aeniceps* present in southern India and Sri Lanka, but no specimens were seen during the course of this study to support this.

Hosts: Unknown.

Key to Species: Partial key given below. The type specimens of *leai* Dodd and *lodgei* Girault were not examined, and therefore cannot be separated in the key from *nigrisaepta* Girault. Additionally, the males of all three species are undescribed, but as whole can be keyed from the males of *aeniceps*. Males thought to be near the newly described species, *viridescens* and *mitteri*, are also keyed below and are discussed further in the *viridescens* section.

Key to the species of *Neapterolelaps* Girault

1.   Female   2

        Male   5

2. (1)   Notauli Y-shaped, joining before posterior scutal margin; shiny black band

present along posterior margin of scutum; apterous, forewing present only as

membranous lump with single long dark bristle (Fig. 37); scutellum slightly

raised and pointed posteriorly (Fig. 38)   *leai* Dodd, *lodgei* Girault,

and *nigrisaepta* Girault

Notauli \ /-shaped (i.e. normal), meeting posterior scutal margin separately (Figs

50, 51); without shiny black band along posterior margin of scutum;

macropterous or brachypterous; scutellum rounded, convex, and gently sloping

postero-ventrally (Fig. 50, 51)   3

3. (2)   Macropterous; epipygium >0.7X remaining metasoma; antenna filiform

aeniceps (Girault)

Brachypterous; epipygium <0.5X remaining metasoma; antenna clavate

4

4. (3)   Head metallic green; metapleuron transversely striate; propodeum irregularly

alveolate (Fig. 50); forewing 0.7X length of mesosoma; submarginal vein with

strong, dark bristles   *viridescens* Desjardins, new

species

Head non-metallic, brownish-orange; metapleuron smooth; propodeum mostly

smooth, lightly wrinkled posteriorly (Fig. 51); forewing 0.3X length of

mesosoma; submarginal vein without strong, dark bristles

mitteri Desjardins, new

species

5. (1) Petiole laterally with brush of white setae along entire length; gastral termites

without thick tufts of white setae laterally   *leai* Dodd, *lodgei* Girault

and *nigrisaepta* Girault

Either petiole bare, or lateral brush of white setae only present on anterior half;

GT4-6 with thick tufts of white setae laterally   6

6. (5) Funicular segments greater than 1.5X as long as wide, with erect setae longer than

width of funicular segment

aeniceps Girault

Funicular segments less than 1.5X as long as wide, with erect setae shorter than

width of funicular segment   near *viridescens* Desjardins,

new species and *mitteri*

Desjardins, new species

Species of *Neapterolelaps*:

aeneiceps (Girault). AUSTRALIAN: Australia.

Australolaelaps aeniceps Girault 1925: 96. 2 females (syntypes): [Queensland]:

Kuranda, coll. A. P. Dodd. (QM, examined).

leai Dodd. Australian: Norfolk Island.

Neapterolelaps leai Dodd 1924: 168. Holotype female: Lord Howe Island, coll.

A. M. Lea. (SAM, not examined).

lodgei Girault. AUSTRALIAN: Australia (Queensland).

    Neapterolelaps lodgei Girault 1913: 87. Holotype female: Queensland: Mount

    Tambourine, rotting leaves, coll. A. M. Lea. (SAM, not examined).

nigrisaepta Girault. AUSTRALIAN: Australia (Queensland).

    Austrolaelaps nigrisaepta Girault 1929: 2. Holotype females: Cairns, coll. A. P.

    Dodd. (QM, examined).

<div align="center">

Neapterolelaps viridescens Desjardins, New Species

(Fig. 50, 56)

</div>

Type information: Holotype female, ANIC. "35.22S 148.50E ACT, Blundells Ck. 850

m., 3km E Piccadilly Circus, Oct. 1985 Lawrence, Weir and Johnson., flight

intercept/window trough trap."

Description: Female. 3.1 mm. *Color:* Brownish orange with metallic green head and

brown areas as follows: anellus plus F1-7; medial posterior portion of lateral lobe of

mesoscutum; posterior margin of scutellum anterior to frenum; dorso-posterior blotch on

GT1; GT5 except for anterior margin; posterior margin of GT7; ovipositor sheaths.

Head: Subtriangular in frontal view, slightly wider than high (1.2:1); head with short,

white, sparse setae, which are short dorsally, becoming twice as long ventrally; occipital

carina faint, present only as dorsal line; vertex coriaceous becoming coriaceous-reticulate

on upper face to reticulate on lower face; ratio of ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 1.6: 5: 3.4: 1; scrobe high, reaching 4/5 of distance from torulus to midocellus; scrobal basin polished; scrobal walls coriaceous-striate; interantennal carina strong, reaching about 0.4X height of scrobe; toruli separated by 1.5 torulus diameters; antenna strongly clavate; scape about 0.7X eye height; anellus 1.5-2X broader than long; ratio of scape: pedicel: anellus: F1: F2: F3 about 38: 20: 1: 13: 10: 10: 7; F4 as long as broad; F5 slightly broader than long; clypeus poorly delimited.

Mesosoma: Dorsally imbricate, becoming reticulate in posterior region of scutellum; ratio of pronotum: scutum: scutellum: propodeum about 1.7: 2.8: 2.5: 1; row of longer darker setae on medial posterior margin of pronotum; pronotum 1.6-2X wider than long, transversely striate laterally; antero-lateral margin of pronotum with carina reaching 0.3X height of pronotum; scutum wider than long (1.9:1); ratio of scutellum: frenum about 4.1: 1; marginal rim of scutellum with lightly grooved, pitted lamella; metanotum medially with grooved, pitted lamella; propodeum irregularly alveolate; plicae strong, latero-medially pointed and attached to second, semicircular carinae adjacent to postspiracular sulcus; postspiracular sulcus deep, with transverse carinae; spiracle 1.5X own diameter from metanotum; spiracle facing dorsally; callus densely setose, projecting posteriorly beyond postspiracular sulcus; prepectus triangular, not in same plane as pronotum, abutting at about 100º angle; mesepimeron mostly smooth, with transversely striate region near dorsal margin; femoral depression deep, smooth, well defined anteriorly; metapleuron transversely striate; all coxae with clumps of white setae on anterior margins; meso- and metatibias spinose; longer metatibial spur about 1.7X length of shorter, about 3X width of metatibia at point of spur insertion; metabasitarsus 5.5X as

long as wide, about 0.7X length of remaining tarsi; hind coxae distinctly transversely striate; wings brachypterous, forewing about 0.7X length of mesosoma; hind wings sinuate, narrow, with marginal vein, about 0.7X length of forewing; submarginal vein of forewing with 6 strong, dark setae; ratio of submarginal vein: marginal vein 1.7:1. *Metasoma:* About 1.9X length of mesosoma; ratio of GT1: GT2-6:GT7:ovipostor sheaths about 2.3:2.2:1.2:1; GT1 dorsally without setae; GT4-6 each with single transverse row of white setae of uniform density; ovipositor apico-dorsally serrate. **Male:** Unknown, but see below.

Discussion: Although the male of *viridescens*, or the newly described *mitteri*, is not known with certainty, a specimen from Tasmania (ANIC, "41.21S 147.22E, Barrow Ck. 8km NE Nunamara, TAS, 12 Jan – 6 Feb 1983, I.D. Naumann & J.C. Cardale, malaise/ethanol.") probably represents the male of a closely related species. It does not belong to either newly described species, as it differs significantly from these taxa in propodeal and metapleural sculpture. Since the male cannot be positively associated with any females, it is not described at this time. However, characteristics which distinguish this specimen from *aeniceps*, *leai*, *lodgei*t, and *nigrisaepta* are mentioned in the key above.

Etymology: *viridescens*, meaning green, named after the metallic green head present in the species.

Distribution: Southeastern Australia (Australian Capitol Territory).

Hosts: Unknown.

Neapterolelaps mitteri Desjardins, New Species

(Fig. 51, 57)

Type information: Holotype female, ANIC. "41.22S 145.35E, Wandle R. 10km, NNE Waratah, TAS, 1 Feb. 1983, I.D. Naumann & J. C. Cardale, ex. ethanol." 1 paratype female, ANIC "41.23S 147.25E, Mt. Barrow 11km E, by N Nunamara, TAS. 30 Jan 1983, I.D. Naumann & J.C. Cardale, ex. ethanol."

Description: Female. 2.7 mm. *Color:* Brownish orange, with the following areas a lighter brownish yellow: clava, coxae, hind tibia and tarsi, dorsal region of GT7, and the following exceptions: F5 light brown becoming darker through F7, thick longitudinal light brown band on anterior half of GT1, meeting thinner transverse light brown band in middle of GT1; posterior third of dorsal surface and entire ventral surface of GT1 brown, becoming light brown on GT2-5; tips of ovipositor sheaths brown. *Head:* Subtriangular-circular in frontal view, slightly wider than high (1.2:1); head with short, white, sparse setae of uniform length; occipital carina present only as dorsal line; vertex lacunose becoming coriaceous on upper face to irregularly striate on lower face; ratio of ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 2: 4.6: 2.8: 1; scrobe high, reaching 4/5 of distance from torulus to midocellus; scrobal basin polished; scrobal walls coriaceous; interantennal carina weak, reaching about 0.3X height of scrobe; toruli separated by 1.4 torulus diameters; antennae weakly clavate; scape height subequal to eye height; anellus about 3X broader than long; ratio of scape: pedicel: anellus: F1: F2: F3 about 23: 12: 1: 7: 7: 6; F4 slightly longer than broad; F5 as

long as broad; clypeus poorly delimited. *Mesosoma:* Dorsally coriaceous-imbricate, becoming imbricate on scutellum; ratio of pronotum: scutum: scutellum: propodeum about 1.3: 2: 1.7: 1; mesosoma covered in fine, white setae; row of slightly longer setae on latero-posterior margins of pronotum; pronotum about 1.7X wider than long, sparsely and irregularly striate laterally; antero-lateral margins of pronotum with faint carina reaching 0.3X height of pronotum (may be mistaken for vertical striae); scutum wider than long (1.7:1); ratio of scutellum: frenum about 4.3:1; marginal rim of scutellum with lightly grooved, pitted lamella; metanotum medially with grooved, pitted lamella; propodeum mostly smooth, posteriorly lightly wrinkled; nucha irregularly transversely striate; plicae strong, pointing laterally; postspiracular sulcus with sparse, white setae, forming a dense row along posterior and medial (plical) margins, setae arching toward callus; setae on inner margin of callus arching toward plicae, forming a cylindrical tunnel around sulcus; postspiracular sulcus deep, mostly smooth, slightly rough posteriorly; spiracle 1.6X own diameter from metanotum; callus densely setose, projecting posteriorly beyond postspiracular sulcus; prepectus triangular, not in same plane as pronotum, abutting at about 100º angle; mesepimeron smooth, with divoted region near dorsal margin between fore and metawing insertions; femoral depression deep, smooth ,well defined anteriorly; metapleuron smooth; all coxae with clumps of white setae on anterior margins; meso- and metatibias spinose; longer metatibial spur about 2.1X length of shorter, about 2.7X width of metatibia at point of spur insertion; metabasitarsus about 6X as long as wide, about 0.7X length of remaining tarsi; hind coxae faintly transversely striate; wings brachypterous, forewing about 0.3X length of metasoma; hind wings small, round, membranous, about 0.35X length of forewing; forewing without strong, dark

setae; ratio of submarginal vein: marginal vein 3.3:1. *Metasoma:* About 1.8X length of mesosoma; ratio of GT1: GT2-6:GT7:ovipostor sheaths about 6.9:2.8:1.8:1; GT1 dorsally with sparse, white setae; GT4-6 each with single transverse row of white setae, sparse medially and denser laterally; ovipositor apico-dorsally serrate. **Male:** Unknown.

Etymology: named for my advisor, Dr. Charles Mitter, who assistance was invauable in the completion of my dissertation.

Distribution: Tasmania.

Hosts: Unknown.

<div align="center">

Netomocera Boucek

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Netomocera Boucek 1954: 49-50. Type species: *Netomocera setifera* Boucek (orig.

     desig. and by monotypy).

Diagnosis: *Netomocera* females are easily identified as they are the only diparines with a strongly asymmetrical clava. The female of *Netomocera* is most likely to be confused with *Chimaerolelaps*. *Netomocera* has a very short petiole (broader than long) and 2 pairs of scutellar bristles, while *Chimaerolelaps* has a long petiole (at least 2X as long as broad) and 3 pairs of scutellar bristles. The male of *Netomocera* can be identified by a combination of features. First, it has bristles on the vertex and dorsal surface of the mesosoma, similar to males of *Dipara* and *Lelaps*. The male of *Netomocera* can be distinguished from both genera by having a short petiole (at most as long as wide),

whereas *Dipara* and *Lelaps* have long petioles (>2X longer than wide). Additionally, the male of *Lelaps* has a median clypeal tooth while the male of *Netomocera* does not.

Discussion: *Netomocera* is resolved at sister-group to the *Lelaps* clade, although there is little evidence in the phylogenetic analysis to support this. The *Lelaps* clade has an F1 at least 1.5X as long as F2, and this character is variable in *Netomocera* (although *Netomocera* usually has an F1 subequal in length to F2, undescribed species have been observed with an elongate F1). Therefore, this feature is synapomorphic for the group in 1 of 2 most parsimonious reconstructions. Additionally, *Netomocera* has a different phylogenetic position in each of the analyses (although it is always fairly basal within Diparinae), and the exact position of *Netomocera* within Diparinae remains uncertain.

Number of Species: 7 described species.

Distribution: Cosmopolitan. Known from all continents except Antarctica.

Hosts: Unknown.

Key to Species: None.

Species of *Netomocera*:

africana Hedqvist. AFROTROPICAL: South Africa.

> *Netomocera africana* Hedqvist 1971: 238-239 (Figs. 1, 2). Holotype female**?**: S. Africa, Pondoland, Port St. John, 6-25 Febr. 1924, coll. R. E. Turner. (BMNH, not examined). 1 female and 3 male paratypes: S. Africa, Pondoland, Port. St.

John, 6-25 Febr. 1924, coll. R. E. Turner. (1 male, BMNH, not examined, 1
female, KHPC, not examined), Dec. 1923, coll. R. E. Turner. (1 male, BMNH,
not examined, 1 male, KHPC, not examined).

alboscapus Hedqvist. AFROTROPICAL: Congo.

Netomocera alboscapus Hedqvist 1971: 238 (Figs. 1,2). Holotype female:
Congo. (KHPC, not examined).

nearctica Yoshimoto. NEARCTIC: Canada.

Netomocera nearctica Yoshimoto 1977: 1044-1048 (Figs. 3, 10, 22, 28).
Holotype female: Chatterton, 13 mi North of Belleville, Ont., 27.V.1968, M63
Top, coll. C. D. Dondale, in meadow. Allotype male: Ottawa, Ont., 3.VI.1940,
coll. O. Peck. (CNC, not examined).

nigra Sureshan & Narendran. ORIENTAL: India.

Netomocera nigra Sureshan & Narendran 1990: 223-224 (Figs. 7-14). Holotype
female: India: Kerala, Calicut University Campus, vii.1986, coll. T. C. Narendran
and party. Allotype male: India: Kerala, Calicut University Campus, i.1986, T. C.
Narendran and party. 1 female and 3 male paratypes: India: Kerala, Peechi,
29.x.1985, T. C. Narendran and party (1 female), India: Kerala, Calicut
University Campus, i.1986 and xii.1986, coll. T. C. Narendran and party (2
males), India: Kerala, Calicut University Campus, 3.v.1988, coll. P. M. Sureshan
(1 male).

rufa Hedqvist. AFROTROPICAL: South Africa.

Netomocera rufa Hedqvist 1971: 241 (Figs. 1, 2). Holotype female: S. Africa,

Pondoland, Port St. John, July 10-31, 1923, coll. R. E. Turner. (BMNH, not

examined).

sedlaceki Boucek. AUSTRALIAN: Australia (Queensland, ACT).

Netomocera sedlaceki Boucek 1988: 336 (Figs. 606-607). Holotype female:

QLD: Brookfiled, nr Brisbane, 9.i.1983, pan trap, coll. Z. Boucek. 20 male and 2

female paratypes: QLD: 1 male, Conway Range nr Proserpine, 2.xii.1976, coll.

Z. Boucek (1 male), Mt Ossa N of Mackay, 28.x.1976, coll. Z. Boucek (1 male),

Mt Archer nr Rockhampton, 4.xii.1976, coll. Z. Boucek (2 males), Cooloola Nat.

Park, vi.1980, coll. J. S. Noyes (9 males), Brookfield, 27.xii.1982, 14. and

18.i.1983, coll. Z. Boucek (4 males and 2 females), Acacia Ridge nr Brisbane,

15.i.1977, coll. Z. Boucek (2 males), Capalaba, 8.vi.1980, coll. J. S. Noyes (1

male), 40 km W of Warwick, 31.x.1976, coll. Z. Boucek (1 male), Mt

Tambourine, 21.xii.1976, coll. Z. Boucek (1 male), Mt Tambourine, x.-xi.1977,

coll. Galloway (4males), Mt. Tambourine, 3.iii.1984, coll. L. Masner (1 male),

Bell Bird Creek, Mt Lamington Nat. Park, 30.v.1966, coll. Z. Liepa (1 male),

ACT: Ainslie, 8.ii.1977, coll. Z. Boucek (1 male). (ANIC, not examined).

setifera Boucek. PALEARCTIC: Eastern Europe.

Netomocera setifera Boucek 1954: 50-53 (Fig. 1). Holotype female: Pouzdrany

in southern Moravia, 3. VI. 1941, coll. Hoffer. 1 allotype and 1 paratype males:

Noutonice-Kováry in Central Bohemia, 6. VI. 1953, coll. Z. Boucek. 5 male

paratypes: Cejc, VII. 1940, and Turold in Pavlov Hills, 10. VII. 1952, in southern

Moravia. (NMP, not examined).

<center>*Nosodipara* Boucek</center>

<center>(Fig. 66)</center>

Nosodipara Boucek 1988: 330-331. Type species: *Nosodipara monteithorum* Boucek

(orig. desig. and by monotypy).

Diagnosis: Female *Nosodipara* are uniquely recognized by having 5 anelli (antennal

formula 11533). In addition, a combination of two characters also defines the genus.

First, they have a large, transverse, black cavity on the mesosternum. Females of the

genus *Pseudoceraphron* also possess this cavity. Generally this cavity is mostly covered

by the pronotum and procoxae and only visible laterally, although in *Nosodipara*

monteithorum the cavity is exposed and clearly visible. Also, female *Nosodipara* possess

a conical scutellum which is postero-laterally compressed and tooth-like. The only other

genera with conical scutella are the African *Pyramidophoriella*, *Conodipara*,

Conophorisca, and some *Dolichodipara*, which all lack the mesosternal cavity. The male

Nosodipara is unknown, although it is suspected to be similar to the male *Dipara*.

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Discussion: *Nosodipara* forms a clade with *Pseudoceraphron* in all phylogenetic analyses. This clade is strongly supported by 7 synapomorphies: a clubbed antennae, a micropilose clava, Y-shaped notauli, a flat and wide propodeum, a vertical postspiracular sulcus, presence of a mesepisternal depression, and the loss of metacoxal striations. Only the notaular form and loss of striations are homoplastic in the analysis. It is unclear whether or not *Nosodipara* represents a monophyletic taxon. It appears paraphyletic in the morphological analysis (*Nosodipara ferrana* positioned as sister-taxon to *Pseudoceraphron*), based on *Nosodipara ferrana* sharing reduced and convex axillae with *Pseudoceraphron regieri*. However, this character is transformed multiple times in the *Nosodipara* and *Pseudoceraphron* clade. Additionally, bristle presence/absence supports the paraphyly of *Nosodipara* in one of two most parsimonious reconstructions. However, bristles are sporadically lost and regained throughout the clade. Therefore the evidence for *Nosodipara* is somewhat tenuous.

Alternatively, monophyly of *Nosodipara* would be supported by the presence of 5 anelli, although this may represent an intermediate in a transformation series from the single anellus of *Pyramidophoriella* to the 7 anelli present in *Pseudoceraphron*. Many other characters differentiate *Nosodipara* from *Pseudoceraphron* in a diagnostic sense. However, they all appear sympleisiomorphic in the analysis (e.g., a laterally bulging pronotum). As the support for *Nosodipara* paraphyly is limited, the taxonomy of the genus will remain the same. In addition to the inconclusive phylogenetic evidence, synonymizing *Nosodipara* with *Pseudoceraphron* would unite two taxa with extreme morphological differences (*Pseudoceraphron* is defined by 7 synapomorphies, 6 of them non-homoplastic). Alternatively, creating a new genus for *Nosodipara ferrana* would set

a precedent for the description of newly discovered species of *Nosodipara* as separate genera.

Number of Species: 2 described (northern Queensland), and possibly 1 undescribed similar to *monteithorum* (southern Queensland).

Distribution: Queensland, Australia. Found in rainforest litter.

Hosts: Unknown.

Key to Species: given below.

<center>**Key to the species of *Nosodipara* Boucek**</center>

1.   Vertex without strong, dark bristles; F2 longer than F1

                                        Nosodipara monteithorum

                                        Boucek

        Vertex with strong, dark bristles; F2 reduced, shorter than F1

                                        Nosodipara ferrana

                                        Desjardins, new species

Species of *Nosodipara*:

monteithorum Boucek. AUSTRALIAN: Australia (Queensland).

> *Nosodipara monteithorum* Boucek 1988: 331. Holotype female: QLD: Plateau S
>
> of The Head, via Killarney, rainforest pitfall trap, 17.xi.1974, coll. G. and S.
>
> Monteith. (ANIC, not examined).

<div align="center">

Nosodipara ferrana Desjardins, New Species

(Fig. 66)

</div>

Type information: Holotype female, QM "Aust: QLD: NE: West, Claudia R, Iron
Range, 4 Dec 1985, G. Monteith. QM Berlesate No. 691, 12.45S 143.14E, Rainforest
50m, sieved litter." 1 Paratype female with same data except "3 Dec 1985. QM Berlesate
No. 690."

Description: Female. 1.4 mm. *Color:* Mostly pale yellowish to orangish brown, with the
following exceptions: clava white; flagellar segments 6-8, and to a lesser extend 5,
brown; ventral third of mesepimeron orangish brown; small circle anterior to cercus
brown. *Head:* Subcircular in frontal view; about 1.3X as high as wide; eyes bare; vertex
with 2 long and 4 short strong, dark setae; head with sparse, white setae, becoming
slightly more dense and twice as long ventrally; head mostly smooth, ocellar triangle and
occiput coriaceous; lateral ocelli connected by dark carina; ratio of ocellocular:
postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 2:8:5:1; scrobe

height about 0.75X distance from toruli to mid-ocellus; scrobal basin and walls

coriaceous; interantennal area with wide carina reaching about 0.5X height of scrobe,

continuing as weakly raised band to top of scrobe; toruli separated by about 1.75 torulus

diameters; scape about 0.8X eye height; A1 3X as broad as long to A5 1.3X as broad as

long (only flagellar segments 6 and 8 appearing to have mps); ratio of scape: pedicel: A1:

A2: A3: A4: A5: F1: F2: F3 about 20:9:1:2:2.5:2.5:3:5:3:5; clypeus strongly delimited

laterally, weakly delimited dorsally. *Mesosoma:* pronotum and scutum dorsally

imbricate, scutellum granulose; ratio of pronotum: scutum: scutellum: propodeum about

2:3:2:1; pronotum posteriorly with a row of long, thin, white setae, these setae also

sparsely present on scutum and scutellum; pronotum 2.3X as wide as long; pronotum

postero-laterally with smooth, depressed area; scutum 1.7X as wide as long; scutellum

slightly conical, gently rounded anteriorly and sharply rounded posteriorly; scutellum

angled, with level of propodeum below level of scutum; posterior scutellar margin

smooth; metanotum thin, smooth, depressed, most apparent posterior to axillae and

medial region of scutellum; propodeum anteriorly with thin, smooth band, separated from

remainder of finely areolate sculptured propodeum by carinate edge; plica absent;

postspiracular area smooth, flat, facing postero-laterally; sulcus between postspiracular

area and metapleuron vertical; spiracle 4X its own diameter from metanotum, facing

postero-laterally; callus absent; prepectus triangular, not in same plane as prontum,

abutting at about 135° angle; mesepimeron smooth, slightly depressed (mesepimeron =

femoral depression), triangular in shape with longest side against metapleuron;

metapleuron smooth; 1 metatibial spur, length about 1.5X width of metatibia at point of

insertion; metabasitarsus 2.7X as long as wide, about 0.5X as long as remaining tarsi;

metacoxa without striations; all coxae bare; metatibia spinose; apterous, forewing present as membranous lump with single strong, protruding bristle, hindwing completely absent. *Metasoma:* About 2.2X length of mesosoma; petiole short, broader than long, granulose; ratio of GT1:GT2-6:GT7:ovipositor sheaths about 3.9:2.6:1.4:1; setae sparsely distributed across GT1 and 7; ovipositor tip covered by sheaths. **Male:** Unknown.

Etymology: *ferra-*, meaning iron, from the Iron Range locality in which it was collected.

Distribution: Australia: Far North Queensland.

Hosts: Unknown.

Pseudoceraphron Dodd

(Figs. 42-49, 67-69)

Pseudoceraphron Dodd 1924. Type species: *Pseudoceraphron pulex* Dodd.

Dipareta Boucek 1988: 332. Type species: *Dipareta albifrons* Boucek (orig. desig. and by monotypy). **New synonymy.** [Type specimen of genus examined]

Malinka Boucek 1988: 333. Type species: *Malinka nana* (orig. desig. and by monotypy). **New synonymy.** [Type specimen of genus not examined]

Note: Dessart (1967) transferred *Pseudoceraphron* from Megaspilinae (Ceraphronidae) to Diparinae.

Diagnosis: *Pseudoceraphron* is most easily identified by the presence of 7 anelli in the female, the eye extended posteriorly beyond the occiput and obscuring the pronotum in lateral view, and a posteriorly concave metacoxa, all of which are unique among Diparinae. All other diparines have at most 5 anelli, an eye which is not extended posteriorly beyond the occiput (pronotum visible in lateral view), and a concave metacoxa.

Discussion: *Pseudoceraphron* is united by 7 synapomorphies, 6 of which are non-homoplastic in the analysis: a carinate posterior genal margin, eye extended posteriorly, 7 female anelli, a wide, flat scutellum wide, a propodeum which is depressed lateral to the plicae, concave metacoxae, and an anteriorly pinched GT1. Historically, Boucek (1988) separated his genera *Dipareta* and *Malinka* from *Pseudoceraphron* Dodd based primarily on notaular structure and bristle patterns. While notaular structure supports monophyly of *Malinka* Boucek and *Pseudoceraphron* Dodd in the phylogenetic analysis, newly described species show variability in the bristle patterns within and between these groups. *Dipareta* Boucek is supported as paraphyletic in the analysis. *Dipareta albifrons* Boucek is sister-group to *Pseudoceraphron* Dodd + *Malinka* Boucek based on two synapomorphies: loss of the acropleuron expansion and the axillae. Therefore, *Dipareta* Boucek and *Malinka* Boucek are herein synonymized with *Pseudoceraphron* Dodd, based on the strong evidence for monophyly of the whole clade, reduced evidence for monophyly of *Pseudoceraphron* Dodd and *Malinka* Boucek, and evidence for the paraphyly of *Dipareta* Boucek.

Boucek (1988) diagnoses, but does not describe, a male specimen from the ANIC which he states does not belong to the species *albifrons* but does belong to *Dipareta*. This specimen resembles a small *Dipara* male but has a reduced number of flagellar segments (8 flagellar segments excluding the anellus compared to *Dipara*'s 10). However, this specimen cannot be associated for certain with any female, and therefore remains undescribed.

Number of Species: 6 described species (Australia: Queensland, Papua New Guinea, New Caledonia), and many undescribed species from these areas.

Distribution: Queensland, Australia east New Caledonia and north to Papua New Guinea.

Hosts: Unknown.

Key to species: Given below.

Key to species of *Pseudoceraphron* Dodd

1. Propodeum laterally with pair of strong, dark bristles; black, tear-drop shaped markings present lateral to notauli   2

    Propodeum without bristles; scutum uniformly colored without tear-drop shaped markings   3

2. (1)   Occipital margin rounded; scutum laterally with a pair of bristles

Pseudoceraphron nana

Boucek

Occipital margin carinate; scutum without bristles   *Pseudoceraphron fijensis*

Desjardins, new species

3. (1)   Notauli widely spaced, subparallel, meeting posterior scutal margin separately;

pronotum not visible in dorsal view   4

Notauli Y-shaped, converging prior to meeting posterior scutal margin; pronotum

visible in dorsal view   5

4. (3)   Without bristles on dorsal surface of mesosoma; occipital margin carinate

Pseudoceraphorn pulex

Dodd

With bristle pairs on the dorsal surface of the pronotum and scutellum; occipital

margin rounded   *Pseudoceraphron burwelli*

Desjardins, new species

5. (3)   Bristles present on vertex but not on scutum; axillae reduced but visible

Pseudoceraphron regieri

Desjardins, new species

Bristles absent from vertex but present on scutum; axillae absent

Pseudoceraphron albifrons

Boucek

Species of *Pseudoceraphron*:

albifrons (Boucek). AUSTRALIAN: Australia, New Zealand.

Dipareta albifrons Boucek 1988: 332. Holotype female and 7 paratype females:

QLD: Bellenden Ker Range, Summit TV Stn., 1560 m, 25.-31.x.1981. One

paratype female collected on 1.-7.xi.1981. coll. G. Monteith. (Holotype in QM,

paratypes in QM and BMNH, examined).

nana (Boucek). AUSTRALIAN: Papua New Guinea.

Malinka nana Boucek 1988:333 (Fig. 605). Holotype female and 2 female

paratypes: PNG: New Ireland, Utu, Liga, 30.vii.1979, coll. J. Bourne. (holotype in

MHNG, paratypes in BMNH and MHNG, examined). 1 female paratype: New

Ireland, Lelet Plateau, Limbin, 24.vii.1979, coll. J. Bourne. (MHNG or BMNH,

not examined).

pulex Dodd. AUSTRALIAN: Lord Howe Island.

Pseudoceraphron pulex Dodd 1924: 174-5. Holotype female: Fallen leaves, Lord

Howe Island, A. M. Lea. SAM, not examined).

<p style="text-align: center">Pseudoceraphron regieri Desjardins, New Species</p>

<p style="text-align: center">(Fig. 67)</p>

Type Information: Holotype female (QM) "Aust: Qld: NE, Mt. Finnigan Summit, 30 Nov 1985, G. Monteith, D. Cook, QM Berlese No. 700, 15.48'S 145.17'E, Rainforest 1100m, Sieved litter." Paratype female (QM) same as holotype.

Description: Female. 1.5 mm. *Color:* Brownish orange with the following exceptions: GT1 brown, becoming dark brown near posterior margin, GT7 anterior to cercus margin dark brown, gena yellowish white, clava + F1 light brown. *Head:* Subtriangular in frontal view, 1.5X as wide as high; eyes bare; head with 6 stout, dark bristles posterior to occipital margin; occipital margin sinuously carinate, carina crossing lateral ocelli; head mostly smooth, posterior margin of gena faintly striate, area below toruli faintly striate, with striae circling up to dorsal edge of parascrobal area; ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 3.3:3.3:1.7:1; scrobe present only as indistinct, shallow, gently sloping depression; interantennal carina semicircular, convex, reaching less than 1 torulus diameter above toruli; toruli separated by 1.6 torulus diameters; scape about 0.8X eye height; scape with strong ventral carina; scape laterally bowed outward; A1 about 3X as broad as long to A7 about 4X as long as broad; ratio of scape: pedicel: A1: A2: A3: A4: A5: A6: A7: F1 about 25:10:1:2:2:2:2:2:2:6; clypeus finely delimited. *Mesosoma:* Dorsally mostly smooth, with pronotum coriaceous and lateral lobes of mesoscutum faintly coriaceous; with long, dark setae sparsely covering

<p style="text-align: center">157</p>

dorsal surface; ratio of pronotum: scutum: scutellum: propodeum about 1.3:1.9:1.1:1; pronotum 3.3X wider than long; pronotum barely visible laterally; scutum 2.4X wider than long; notauli deeply pitted with transverse carinae; axillae very small, flat, present only at anterio-lateral corners of scutellum; scutellum mostly flat (slightly raised posteriorly), with scutum and propodeum at the same level; posterior scutellar margin smooth; metanotum present as triangular sclerite lateral and posterior to axilla, not visible posterior of scutellum; propodeum mostly smooth, raised and rounded medially for insertion of petiole; plicae strong; postspiracular area smooth, flat, facing postero-laterally; sulcus between postspiracular area and metapleuron vertical; spiracle 4X its own diameter from metanotum, facing postero-ventrally; callus absent; prepectus triangular, not in same plane as pronotum, abutting at about 135° angle; mesepimeron smooth, slightly depressed (mesepimeron = femoral depression), bulging anteriorly ventral to acropleuron, 3.2X as high as wide; metapleuron smooth, depressed posteriorly; one metatibial spur, 1.7X width of metatibia at point of insertion; metabasitarsus about 2.8X as long as wide, about 0.5X length of remaining tarsi; metacoxa without transverse striae, mostly bare anteriorly except for few setae near distal end; meso- and metatibia not spinose; apterous, forewing reduced to membranous stump with single long, dark, protruding bristle, hindwing apparently absent. *Metasoma:* 2.4X length of mesosoma; petiole smooth, short, about 2X as broad as long; ratio of GT1: GT2-6: GT7: ovipositor sheaths about 6.5:1:1:1; anterior half of GT1 with long, dark setae (similar to dorsal mesosomal setae) sparsely covering dorsal and dorso-lateral surface, posterior half with lighter, more widely spaced setae; ovipositor smooth and pointed. **Male:** Unknown.

Etymology: Named for one of my committee members, Dr. Jerome Regier, whose guidance was invaluable in the completion of the molecular component of my dissertation.

Distribution: Australia: Queensland.

Hosts: Unknown.

Pseudoceraphron burwelli Desjardins, New Species

(Figs. 42-49, 69)

Type Information: Holotype female (QM) "New Caledonia 9913, 22.03'Sx166.28'E, Mt Dzumac road, 700m, 1 Dec 2000, G.B. Monteith, Pyrethrum, trunks & logs." Paratype female (QM) "New Caledonia 9901, 22.05'Sx166.22'E, Mt Mou, base, 200m, 23 Nov 2000, G.B. Monteith, Pyrethrum, trunks & logs." Paratype female (QM) "New Caledonia 9919, 21.45'Sx166.00'E, Mt Do Summit, 1000m, 21 Nov 2000, G.B. Monteith, Pyrethrum, trunks & logs." Paratype female (QM) "New Caledonia 9931, 22.11'Sx166.01'E, Mt Koghis, 500m, 22 Nov 2000, G.B. Monteith, pyrethrum, trunks & logs."

Description: Female. 1.2 mm. *Color:* Brownish black with the following exceptions: head bluish black, scape mostly brownish yellow, distal 1/4 of scape + flagellum brown, mandibles brownish orange, tibia proximally dark brown, lightening to brownish yellow distally, tarsi proximally brownish yellow, darkening to brown distally, GT7 posterior to cercus brownish yellow, ovipositor sheath yellow anteriorly, dark brown posteriorly,

ovipositor yellow. *Head:* Subtriangular in frontal view, 1.25X as wide as high; eyes bare; occipital margin carinate, carina posterior to lateral ocelli; head mostly smooth, posterior margin of gena faintly striate, area around torulus with faint, circular striae; ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 4:12:6.4:1; scrobe present only as indistinct, shallow, gently sloping depression; interantennal area slightly convex; toruli separated by 2 torulus diameters; scape about 0.9X eye height; scape without strong ventral carina; scape laterally bowed outward; A1 about 3X as broad as long to A7 about 4X as long as broad; ratio of scape: pedicel: A1: A2: A3: A4: A5: A6: A7: F1 about 21:6:1:1:1:1:1:1:1:3; clypeus poorly delimited. *Mesosoma:* Dorsally coriaceous; mostly bare, except for a few pairs of thin, white setae, and 2 medial scutal and 2 posterior scutellar bristles; ratio of scutum: scutellum: propodeum (pronotum entirely obscured) about 2.3:2.2:1; scutum 3.2X wider than long; notaular grooves smooth; axilla only indicated by diagonal sulcus at antero-lateral edge of scutellum; scutellum flat, with scutum at slightly higher level than propodeum; posterior scutellar margin smooth; metanotum absent; propodeum smooth medially, coriaceous laterally, raised medially for insertion of petiole with longitudinal carina delimiting lateral edge of raised area; plica strong, propodeum strongly depressed lateral to plica; postspiracular area smooth, flat, facing postero-laterally; sulcus between postspiracular area and metapleuron vertical; spiracle 5X its own diameter from metanotum, facing postero-ventrally; callus absent; prepectus triangular, in similar plane as pronotum; mesepimeron smooth, slightly depressed (mesepimeron = femoral depression), diamond-shaped, 4.5X as high as wide; metapleuron smooth, depressed medially; one metatibial spur, 0.6X width of metatibia at point of insertion;

metabasitarsus about 1.7X as long as wide, about 0.2X length of remaining tarsi; metacoxa without transverse striae, mostly bare anteriorly except for few setae near distal end; meso- and metatibia not spinose; apterous, forewing reduced to membranous stump with single long, dark, protruding bristle, hindwing apparently absent. *Metasoma:* 3.4X length of mesosoma; petiole smooth, short, about 2.3X as broad as long; ratio of GT1: GT2-6: GT7: ovipositor sheaths about 10.8:2:1:1.5; metasoma dorsally with sparse, fine, white setae; ovipositor smooth and pointed. **Male:** Unknown.

Etymology: Named for Chris Burwell, who generously hosted my visit to the Queensland museum, provided a large amount of mounted Australian material, and was invaluable in assisting in my collection of many of the taxa used in the molecular portion of my dissertation.

Distribution: New Caledonia.

Hosts: Unknown.

Pseudoceraphron fijensis Desjardins, New Species

(Fig. 68)

Type Information: Holotype female (QM) "Fiji: Kadavu. Mt, Korogatule, 300m, near Matasawalevu, 4-7 July 1987, G. Monteith/Pyrethrum/Logs, Trees." Paratype female (QM) "Fiji: Viti Levu, Nadarivatu Reserve, 11 July 1987, G. Monteith, QM Berlese No. 775, 17.34'S 177.57'E, Rainforest, 800m, sieved litter."

Description: Female. 1.4 mm. *Color:* Head, pronotum, scape, clava light brownish yellow; pedicel, A5-7, F1 brown; A1-4, eye white; pronotum and scutum brownish orange; scutum with tranverse tear-drop shaped bands lateral to notauli; propodeum brown; mesosoma laterally brown; legs mostly brownish orange, metatibia off-white; GT1-6 brown dorsally, becoming brownish orange ventro-laterally; GT7, ovipositor sheath mostly white, apex of ovipositor light brown. *Head:* Subtriangular in frontal view, 2X as wide as high; eyes bare; occipital margin carinate, carina at lateral ocelli; head smooth; ocellocular: postocellar: mid-to-lateral ocellus distance: lateral ocellus diameter about 9.3:8:3.3:1; scrobe present only as indistinct, shallow, gently sloping depression; interantennal area carinate, carina not extending dorsally into scrobal depression; toruli separated by 1.2 torulus diameters; scape about 0.8X eye height; scape with strong ventral carina; scape laterally bowed outward; A1 about 2.5X as broad as long to A7 about 2X as long as broad; ratio of scape: pedicel: A1: A2: A3: A4: A5: A6: A7: F1 about 28:10:1:1:1:1:1:1.5:2:2.5; clypeus well delimited. *Mesosoma:* Dorsally mostly smooth, scutellum finely coriaceous; mostly bare, except for 2 posterior scutellar bristles; ratio of pronotum (partially obscured): scutum: scutellum: propodeum about 1.4:3:1:1.1; pronotum (visible portion) 4.5X wider than long; scutum 2.6X wider than long; notauli transverse anteriorly, turning posteriorly at anterior margin of tear-drop shaped black markings and proceeding parallel to posterior scutal margin; notaular grooves smooth; axilla absent; scutellum flat, emarginated medially by scutum, at same level as propodeum; posterior scutellar margin smooth; metanotum absent; propodeum coriaceous, raised medially for insertion of petiole with longitudinal carina delimiting lateral edge of raised area; plica strong, propodeum strongly depressed lateral to plica,

with single bristle pair on lateral edge of depressed area; postspiracular area smooth, flat, facing postero-laterally; sulcus between postspiracular area and metapleuron vertical; spiracle not visible; callus absent; prepectus not visible; mesepimeron smooth, slightly depressed (mesepimeron = femoral depression), diamond-shaped, 5.3X as high as wide; metapleuron smooth, depressed medially; one metatibial spur, 1.5X width of metatibia at point of insertion; metabasitarsus about 2.3X as long as wide, about 0.3X length of remaining tarsi; metacoxa without transverse striae, bare; meso- and metatibia spinose; apterous, forewing and hindwing apparently absent. *Metasoma:* 5.7X length of mesosoma; petiole smooth, barely visible, about 6X as broad as long; propodeum mostly smooth but coriaceous antero-dorsally; propodeum with longitudinal invaginations just posterior to lateral margins of petiole insertion; ratio of GT1: GT2-6: GT7: ovipositor sheaths about 5.4:2.6:1.3:1; metasoma dorsally with sparse, fine, white setae; ovipositor smooth and pointed. **Male:** Unknown.

Etymology: Named after the island of Fiji, on which the specimen was collected.

Distribution: Fiji.

Hosts: Unknown.

Pyramidophoriella Hedqvist

(Figs. 54-55)

Pyramidophoriella Hedqvist, 1969: 178-179. Type species: *Pyramidophoriella albiclava* Hedqvist (orig. desig.).

Diagnosis: *Pyramidophoriella* has a propodeum with 2 large dorso-lateral horns, with propodeal spiracles situated on the lateral surface of horns (Fig. 55). Although most diparines lack these horns completely, smaller dorso-lateral propodeal projections have been noted in some species of *Lelaps*. In these cases, however, the spiracles are not situated on the horns. Additionally, *Pyramidophoriella* completely lacks notauli. Aside from *Pyramidophoriella*, the only diparine which has been recorded as lacking notauli is *Dipara machadoi*. However, the type specimen of the latter taxon could not be located to verify the description.

Discussion: *Pyramidophoriella* is resolved at the base of the clade containing *Nosodipara* and *Pseudoceraphron* based on 1 synapomorphy, the anterior expansion of the tegula. This relationship suggests that *Nosodipara* and *Pseudoceraphron* were part of a recolonization of Australia from Africa, and they are nested deep within a clade of genera endemic to Africa.

Species of *Pyramidophoriella*:

albiclava Hedqvist. AFROTROPICAL: South Africa.

> *Pyramidophoriella albiclava* Hedqvist 1969: 179 (Figs. 2, 3). Holotype female:
> S. Africa, Pondoland, Port St. John, July 10-31, 1923, coll. R. E. Turner. (BMNH,
> not examined). 19 female paratypes: Pondoland, Port St. John, Feb. 6-25, 1924 (5
> females), Jan, 1924 (5 females), 18-31 Mar. 1924 (1 female), 1-17 Mar. 1924 (1

female), July 10-31 1923 (1 female), Sept. 1923 (1 female), E. Cape Prov.

Katberg, 4000 ft. Oct. 1932 (1 female), Cape Prov., Somerset East, 1-26, i.1931

(1 female), and Cape Prov., Somerset East, Nov. 1930 (2 females). (BMNH and

KHPC, not examined).

brunnea Hedqvist. AFROTROPICAL: South Africa.

Pyramidophoriella brunnea Hedqvist 1969: 179-180 (Fig. 3). Holotype female:

S. Africa, Pondoland, Port St. John, 6-25 Febr. 1924, coll. R. E. Turner. (BMNH,

not examined).

Taxa removed from the Diparinae

Calolelaps Timberlake

Calolelaps Timberlake 1925: 184-186. Type species: *Calolelaps basalis* Timberlake

(orig. desig.).

Discussion: The three Hawaiin genera *Calolelaps*, *Neolelaps*, and *Stictolelaps* (and to a

lesser extent *Mesolelaps*) possess no characters that would suggest their inclusion within

Diparinae. They lack the cercal brush, dorsal bristles, hind coxal striations, expanded

GT1, and single anellus, in addition to having a convex dorsellum, any of which may hint

at inclusion within Diparinae. *Mesolelaps* does possess an expanded GT1 and single

anellus, although it lacks both diparine synapomorphies: presence of a cercal brush and

absence of a convex dorsellum. These genera were likely initially placed within

Diparinae because they share a median clypeal tooth with *Lelaps*. The removal of

Mesolelaps from Diparinae and subsequent placement in the Pteromalinae +

Miscogasterinae clade would make *Mesolelaps* the only genus in that group with a single

anellus.

Yoshimoto (1967) discussed the phylogenetic placement of the Hawaiin genera,

which he treated as members of Miscogasterinae. However, he made no formal

declaration of their transfer from Diparinae to Miscogasterinae, and in fact made no

mention of Diparinae whatsoever. An examination of the original descriptions (Ashmead

1904, 1901; Timberlake 1925) shows that both authors originally placed these genera in

"Lelapinae." Boucek (1988) treated *Mesolelaps* as an extralimital genus of Diparinae,

and made no statement about the remaining genera or the placement of any of the genera

in Miscogasterinae. Additionally, Yoshimoto (1967) stated that "*Calolelaps* Timberlake

(=*Stictolelaps* Timberlake)." However, he made no declaration of synonymy there either.

Yoshimoto, in an unpublished manuscript dated later than his 1967 paper, treated

Calolelaps and *Stictolelaps* as separate genera, and described a new species of

Stictolelaps. In this manuscript Yoshimoto planned to remove these four genera and

place them in their own tribe, Neolelapini. He also stated that these genera were

associated with the tribes Miscogasterini and Trigonoderini. Paul Hanson (pers. comm.)

also suggested that these specimens share a similar habitus with Trigonoderini, although

they lack characters to place them in either of the trigonoderine clades as defined by

Heydon (1997). *Calolelaps* is herein removed from Diparinae and placed in

Miscogasterinae, without tribal affiliation.

The holotype female of *Calolelaps basalis* is heavily damaged, with only two legs remaining on the point mount and the rest of the specimen lost. However, the allotype male remains entirely intact, and the taxonomic decisions made here are based on that specimen. The holotype of *Calolelaps coeruleus* appears to be lost. Although it was recorded to be housed in the Bishop Museum, there is no unit tray there to mark its presence now or in the past. No record has been found of it at any other museum.

Species of *Calolelaps*:

basalis Timberlake. OCEANIAN: Hawaii.

> *Calolelaps basalis* Timberlake 1925: 186-188 (Fig. 6). Holotype female: [Hawaii]: Mount Kaala, Oahu, at 2000 ft. elevation, from *Eragrostis grandis*, May 18, 1920. coll Timberlake. Allotype male: [Hawaii]: Palolo, Oahu, 2000 ft., 1903. coll Perkins. (BISH, examined).

coeruleus Timberlake. OCEANIAN: Hawaii.

> *Calolelaps coeruleus* Timberlake 1925: 188-189. Holotype female: Hawaii: Kealakekua, Kona, at 3500 ft. elevation, from *Myoporum sandwicense*, August 11, 1919. coll. Timberlake. (type location unknown).

Dinarmolaelaps Masi

Dinarmolaelaps Masi 1917: 172. Type species: *Dinarmolaelaps protus* Masi (by monotypy).

Discussion: Based on examination of the holotype specimen, *Dinarmolaelaps* belongs near or within *Homoporus* (R. Burks, pers comm). The holotype of *Dinarmolaelaps vatomandryi* is missing both the head and gaster. The thorax bears little resemblance to that of *D. protus*, and it is difficult to speculate on the relationship between the two taxa. *Dinarmolaelaps* is herein removed from Diparinae and placed in Pteromalinae.

Species of *Dinarmolaelaps*:

protus Masi. AFROTROPICAL: Seychelles.

> *Dinarmolaelaps protus* Masi 1917: 172-173. 2 males and one female (desig. uncertain). 'Silhouette: Mare aux Cochons.-Mahé: "cultivated country at about 1,000 ft."'. (BMNH, examined).

vatomandryi Risbec. AFROTROPICAL: Madagascar.

> *Dinarmolaelaps vatomandryi* Risbec 1952: 325-325 (Fig. 53). Holotype male: Vatomandry, VIII, 1940. coll. A. Seyrig. (Paris Museum, examined).

Liepara Boucek

Liepara Boucek 1988: 327-328. Type species: *Liepara dentata* Boucek (orig. desig.).

Discussion: The genus *Liepara* Boucek is herein removed from the Diparinae, and positioned within the Pteromalidae as an unplaced genus. The phylogenetic position of *Liepara* is discussed in the phylogenetic analysis section.

Species of *Liepara*:

dahmsi Boucek. AUSTRALIAN: Australia (Queensland).

> *Liepara dahmsi* Boucek 1988: 328. Holotype female and 2 female paratypes: QLD: Cooloola Nat. Park, 10.x.1979, coll. E. C. Dahms. (holotype and 1 paratype in QM, 1 paratype in BMNH, examined).

dentata Boucek. AUSTRALIAN: Australia (New South Wales, Victoria).

> *Liepara dentata* Boucek 1988: 328. Holotype female: NSW: Cudmirah Reserve NNE of Milton, 14.iv.1968, coll. Z. Liepa. (ANIC, examined). 2 female and 1 male paratypes: VIC: Black's Spur E of Melbourne, 5.ii.1983, coll. Z. Boucek. (BMNH, examined).

Mesolelaps Ashmead

Mesolelaps Ashmead 1901: 313. Type species: *Mesolelaps cyaneiventris* Ashmead (orig. desig. and by monotypy).

Discussion: *Mesolelaps* is herein removed from Diparinae and placed in Miscogasterinae, without tribal affiliation, based on the reasoning discussed in the generic entry for *Calolelaps*.

Species of *Mesolelaps*:

cyaneiventris Ashmead. OCEANIAN: Hawaii.

  Mesolelaps cyaneiventris Ashmead 1901: 313-314 (Plate 8, Fig. 8). Type

  information uncertain: "Hawaii: Kilauea; Kona, taken in August, September, and

  November; Olaa, in November." (USNM, examined).

Neolelaps Ashmead

Neolelaps Ashmead 1901: 312. Type species: *Neolelaps hawaiiensis* Ashmead (orig. desig.).

Discussion: *Neolelaps* is herein removed from Diparinae and placed in Miscogasterinae, without tribal affiliation, based on the reasoning discussed in the generic entry for *Calolelaps*.

Species of *Neolelaps*:

flavipes Ashmead. OCEANIAN: Hawaii.

> *Neolelaps flavipes* Ashmead 1901: 313 (Plate 8, Fig. 7). Type information
> uncertain: "Kauai (high plateau). Taken in August 1894." (USNM, examined).

hawaiiensis Asmead. OCEANIAN: Hawaii.

> *Neolelaps hawaiiensis* Asmead 1901: 313. Holotype female: "Kauai:
> Koholuamo, in April" (USNM, examined).

Seyrigina Risbec

Seyrigina Risbec 1952: 381. Type species: *Seyrigina gracile* Risbec (by monotypy).

Discussion: The holotype of *Seyrigina gracile* is missing both the head and gaster. However, the tarsi are four segmented, and the specimen appears to belong to Eulophinae (Eulophidae). *Seyrigina* is therefore transferred to the Eulophinae (Eulophidae). The

holotype of *Seyrigina rizicola* is not located at the Paris Museum, and is presumed to be lost.

Species of *Seyrigina*:

gracile Risbec. AFROTROPICAL: Madagascar.

> *Seyrigina gracile* Risbec 1952: 381-383 (Fig. 59). Type designation uncertain : 1 female: Bekily, IX, 1936, coll. A. Seyrig. 1 male: Tananarive, I, 1930, coll. A. Seyrig. (female: Paris museum, examined, male: type location unknown).

rizicola Risbec. AFROTROPICAL: Madagascar.

> *Seyrigina rizicola* Risbec 1960: 169-171 (Fig. 2). Holotype female: "1 femelle récolté sur riz. II.1949. Tsimbazaza. Renaud Paulian." (type location unknown).

<div align="center">

Stictolelaps Timberlake

</div>

Stictolelaps Timberlake 1925: 189-190. Type species: *Stictolelaps flaviventris* Stictolelaps (orig. desig.).

Discussion: *Stictolelaps* is herein removed from Diparinae and placed in Miscogasterinae, without tribal affiliation, based on the reasoning discussed in the generic entry for *Calolelaps*.

flaviventris Timberlake. OCEANIAN: Hawaii.

> *Stictolelaps flaviventris* Timberlake 1925: 190-191 (Fig. 7). Holotype female:
>
> Nunanu Pali, Oahu, 1904, coll. Perkins. Allotype male: Palolo Hill trail, Oahu,
>
> April 9, 1916, coll. Timberlake. (BISH, examined).

stigmatus Timberlake. OCEANIAN: Hawaii.

> *Stictolelaps stigmatus* Timberlake 1925: 191-192 (Fig. 8). Holotype male: Niu
>
> ridge, Oahu, Feb. 10, 1918, coll. Timberlake. (BISH, examined).

Taxa removed from Diparinae and placed in synonymy

Notanisus Walker

Notanisus Walker 1837: 352. Type species: *Notanisus versicolor* Walker (by monotypy).
…(see Gibson 2003)

Bekiliella Risbec 1952: 378. Type species: *Bekiliella cyanea* Risbec (by monotypy).
New Synonymy.

Discussion: *Bekiliella* is known only from the holotype specimen. Two additional

specimens, also labeled "*Bekiliella cyanea*", are located at the Paris Museum. These

additional specimens have distinctly less metallic coloration than the holotype specimen,

and may or may not represent a different species. Regardless, the holotype is congeneric

with *Notanisus*, and Bekiliella is herein synonomized with *Notanisus*.

Species of *Notanisus*:

...(see Gibson 2003)

cyanea (Risbec). AFROTROPICAL: Madagascar.

> *Bekiliella cyanea* Risbec 1952: 378-381 (Fig. 59). Holotype male: [Madagascar]:
>
> Bekily, XI, 1938. coll. A. Seyrig. (Paris Museum, examined).

<center>*Spalangiopelta* Masi</center>

Spalangiopelta Masi 1922: 169. Type species: *Spalangiopelta brachyptera* Masi (by

monotypy).

Diparisca Hedqvist 1964: 54-55. Type species: *Diparisca ferrierei* Hedqvist (orig.

desig. and by monotypy). **New synonymy.**

Discussion: *Diparisca*, known only from the type specimen of *D. ferrierei*, is herein

synonomized with *Spalangiopelta*. That holotype specimen has been examined and

conclusively identified as *Spalangiopelta*. Darling (1991a) mentioned an undescribed

species from Brazil (Nova Teutonia and San Jose Barreiro), but postponed its description

because he only had male material. The holotype of *D. ferrierei* is believed to be the

female associated with the aforementioned male. Additionally, 2 female specimens from

the same locality (and apparently the same species) exist in the collection at the CNC. It

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is possible that the specimens were split up in collections based on their sexual

dimorphism.

Species of *Spalangiopelta*:

...(see Darling 1991a)

ferrierei (Hedqvist). NEOTROPICAL: Brazil.

> *Diparisca ferrierei* Hedqvist 1964: 55-56. Holotype female and paratype female:
>
> Brazil, Nova Teutonia (27°15' B. 52°23' L), December 1962. coll. F. Plaumann.
>
> (holotype: KHPC, examined, location of paratype unknown).

Chapter 2: **Molecular phylogenetics of Pteromalidae (Hymenoptera) using four**

nuclear protein-coding genes

Abstract

Chalcidoidea, one of the largest superfamilies of parasitic Hymenoptera, has

major importance in the biological control of insect pests. However, phylogenetic

relationships both within and between chalcidoid families have been poorly understood,

particularly within Pteromalidae, one of largest chalcidoid families. Forty-two taxa

broadly representing Chalcidoidea and more specifically Pteromalidae were sequenced

for 4620 bp of four nuclear protein-coding genes, including 1719bp of CAD, 708bp of

DDC, 1142bp of enolase, and 1044bp of PEPCK. The combined data set was analyzed

using maximum likelihood methods, and the AU test was used to test support for non-

monophyly of taxonomic groups which appeared para- or polyphyletic in the tree.

Phlyogenetic relationships that have been supported by previous morphological and

molecular evidence were recovered, including the monophyly of Chalcidoidea, the sister-

group relationship of Mymaridae to the remainder of Chalcidoidea, and the basal

placement of *Encarsia* (Aphelinidae) within Chalcidoidea - Mymaridae. Groups well

supported as monophyletic by morphology but resolved as polyphyletic in previous

molecular analyses were recovered here as monophyletic, including Chalcididae,

Eucharitidae + Perilampidae, and Eunotini (Pteromalidae: Eunotinae). The hypothesis of

wood-boring beetle parasitism as the ancestral biology of Chalcidoidea is rejected,

although the alternate hypothesis, egg parasitism, is neither supported nor rejected. The

monophyly of Pteromalidae is strongly rejected (p<0.001) with respect to a number of families, including Chalcididae, Eucharitidae, Eurytomidae, Perilampidae, and possibly Torymidae. The 'pteromalid lineage' of families is generally recovered as monophyletic. The ancestral pteromalid was likely a wood-boring beetle parasitoid, in the form of either Cerocephalinae or Cleonymini (Cleonyminae). New hypotheses are proposed for relationships within the 'pteromalid lineage,' including Eutrichosomatinae (Pteromalidae) as the basal lineage of the perilampid/eucharitid clade, and Colotrechnini (Pteromalidae: Colotrechninae) + Asaphinae (Pteromalidae). Evidence for monophyly of the pteromalid subfamilies Diparinae, Eunotinae, and Cleonyminae was ambiguous, and the monophyly of Colotrechninae was strongly rejected (p<0.001). These results demostrate that nuclear protein-coding genes are a powerful source of data for resolving relationships within Chalcidoidea.

Introduction

Chalcidoidea, one of the largest superfamilies of parasitic Hymenoptera, includes about 22,000 described species (Noyes 2003). The majority of chalcidoids, commonly called chalcids, are parasitoids. They are a conspicuous element in natural foodwebs, and also have major importance in the biological control of insect pests. For example, introduction of the chalcidoid *Neodusmetia sangwani* into the U. S. to control the rhodesgrass mealybug is estimated to have saved at least $200M annually (Dean et al.1979). Yearly savings of up to $250M have resulted from introduction of *Epidinocarsis lopezi* into Africa to control the cassava mealybug (Norrgard 1988a, b). Chalcidoids have also played key roles in the control of such diverse pests as coconut leaf-mining beetle in Fiji, cereal leaf beetle in the U.S., spiny blackfly in Japan, citrus blackfly in Cuba, and soybean looper in the U.S. (Debach and Rose 1991, Puttler et al.1980).

The ability of chalcidoids to control such a diverse array of insect pests is reflected in their broad array of life history strategies. Chalcidoids may be endo- or ectoparasitic, idio- or koinobionts (killing the host immediately or at a later life stage), arrheno- or thelytokous (unfertilized eggs develop into males or parthenogenetically into females), and show tremendous variety in other life history features as well. They are known to parasitize 13 orders of insects, as well as a variety of arachnids and even nematodes. Reversion to phytophagy, primarily gall-forming and seed-feeding, has also occurred in Chalcidoidea. A variety of hypotheses, often conflicting, have been offered about the evolution of chalcid life histories. For example, both egg parasitism (Dowton

and Austin 2001) and ectoparasitism of wood-boring beetles (Boucek 1988) have been argued to be the ancestral chalcidoid habit.

Chalcidoid evolution offers a prominent example of diversification associated with shifts in ecological roles, waiting reconstruction and deconstruction by phylogenetic analysis. A sound phylogenetic classification would also facilitate the use of chalcids in biological control, as the biology of poorly known potential control agents can be predicted in part from knowledge of their close relatives.

Monophyly for Chalcidoidea, which currently contains 20 families (Grissell and Schauff 1997), is well established (Gibson 1986), and a basal position for Mymaridae is supported by both morphological (Heraty et al.1997, Quicke et al.1994) and molecular evidence (Campbell et al. 2000). Despite the ecological and economic importance of Chalcidoidea, however, phylogenetic relationships both within and between chalcidoid families are still largely obscure. Noyes (1990) offered an intuitive scheme of family relatedness, and recent morphological cladistic studies have treated several individual families or small complexes of families (e.g. Heraty and Darling 1984, Woolley 1988, Gibson 1989, Wijesekara 1997, and Heraty 2000).

A central difficulty is the status of the problematic family Pteromalidae, one of the three largest in the superfamily (3506 species; Noyes 2003) and often considered its "garbage can." Pteromalidae is defined only by the absence of features defining other chalcidoid families, and has been speculated to be paraphyletic with respect to a number of these families. These are often referred to collectively as the 'pteromalid lineage,' alternatives being the 'mymarid' and 'eulophid lineages'. The 'pteromalid lineage' is defined here, following Gibson et al. (1999), as chalcidoids with 5 tarsal segments and, to

a lesser degree, with at least 8 flagellar segments and a recurved protibial spur, and is comprised of Agaonidae, Chalcididae, Encyrtidae, Eucharitidae, Eupelmidae, Eurytomidae, Leucospidae, Perilampidae, Pteromalidae, Tanaostigmatidae, and Torymidae (Campbell et. al. 2000). Thirty-one subfamilies are currently recognized within Pteromalidae (Noyes 2003), although inclusion and exclusion of many subfamilies is still highly uncertain. Numerous useful hypotheses have been advanced about relationships among subfamilies (e.g. Boucek 1974, Boucek 1988a, b, Darling 1988, Graham 1969), but none have been subjected to rigorous phylogenetic analysis. A subfamily-level phylogeny for the pteromalids and other associated chalcidoids would therefore be a major step toward better understanding of chalcidoid phylogeny and evolution.

Török and Abraham (2001) conducted the only broad-ranging morphological phylogenetic study of Pteromalidae. Their data set consisted of 90 characters coded for 38 exemplars, representing seven families all belonging to the 'pteromalid lineage.' Eleven subfamilies of Pteromalidae were represented, although the taxon sampling was heavily focused on Pteromalinae and Miscogasterinae (20 taxa). Chalcididae and Eurytomidae were used as outgroups, which is problematic as these families may render Pteromalidae paraphyletic. The positions of many taxa were unstable in their analyses, and although the authors report that Pteromalidae emerged as polyphyletic, they cited no supporting characters. Thus, it is difficult to draw strong conclusions from this study.

Previous molecular studies of relationships within and among chalcid families, based mainly on the widely-used mitochondrial and nuclear ribosomal markers, have yielded limited resolution, particularly with regard to Pteromalidae. Analyses of 28S

rRNA have supported placement of Elasmidae within Eulophidae (Gauthier et al. 2000) and polylphyly of Agaonidae sensu lato (Rasplus et al.1998). However, a study of the same gene region by Campbell et al. (2000), sampling multiple chalcid families and seven pteromalid subfamilies, resolved the basal position of Mymaridae but little else, and failed to recover a number of morphologically well-supported groups. Alignments were problematic in all of these studies. Mitochondrial protein-coding genes have been applied to higher-level hymenopteran phylogenetics (e.g. Dowton and Austin 1995, 2001), but resolution was limited by extreme base compositional heterogeneity across taxa. The generally high A/T content of hymenopteran mitochondria (e.g., ~85% in *Apis mellifera*) also limits the amount the amount of phylogenetic information.

Given this evidence, it seems clear that additional markers are needed to solve problems of hymenopteran phylogeny, including pteromalid/chalcid relationships. Protein-coding nuclear genes are an especially promising source of evidence for insects generally, and have begun to be applied in Hymenoptera. Several studies of this order have included sequences of the nuclear gene elongation factor-1α (EF-1α; Belshaw and Quicke 1997, Belshaw et al. 2000, Dowton and Austin 1998, 2001). Danforth et al. (2004) used *wingless* and long-wavelength opsin, in addition to EF-1α, to resolve Cretaceous-age divergences in bees. Rokas et al. (2002) examined the phylogenetic utility of eight genes in cynipid wasps, including both EF-1α and long-wavelenth opsin, and concluded that the latter show promise for resolving intra-familial divergences within parasitic Hymenoptera.

The study presented here provides the first comprehensive phylogenetic analysis of relationships across the major subfamilies of Pteromalidae and associated chalcids

using nuclear protein-coding genes. At total of 4620 bp were sequenced, from four nuclear protein-coding genes previously shown to be useful in resolving Cretaceous-age divergences in insects. These genes studied were: CAD (part of the *rudimentary* locus; 1719 bp); dopa decarboxylase (DDC; 708 bp), enolase (1142 bp), and phosphoenolpyruvate carboxykinase (PEPCK; 1044 bp). These genes were selected in part on criteria discussed by Friedlander et al. (1992), including probable phylogenetic utility, low apparent copy number, extensive coding regions, and a lack of obvious nucleotide bias and internal repeats. They were also chosen for their complementary rates of divergence, in hopes that they would collectively provide resolution across the varying depths that pteromalid/chalcid phylogeny probably represent.

Taxa were chosen to represent a broad range of families in the 'pteromalid lineage' and subfamilies of Pteromalidae. Multiple representatives from different families, subfamilies, and tribes were chosen both to test the ability of the nuclear protein-coding genes to recover these clades, and to test the monophyly of the taxonomic groups themselves. A broad range of outgroups were chosen which reached from inside to outside the superfamily in order to ensure accurate rooting of the tree.

Methods

Taxon Sampling

Taxa included in the analysis are listed in Table 1. Three outgroups were chosen from outside the superfamily, including one from Ceraphronidae (Ceraphronoidea) and one each from Scelionidae and Platygasteridae (Platygastroidea). Both groups have been previously hypothesized as close relatives of Chalcidoidea (e.g., Dowton and Austin 2001). *Gonatocerus* (Mymaridae) was also included as an outgroup as its basal position within Chalcidoidea is strongly supported. Additional taxa chosen from outside the 'pteromalid lineage' included one eulophid (*Tetrasitchus*) and *Encarsia* (Aphelinidae), which resolved as a basal chalcidoid in the Campbell et. al (2000) analysis based on 28S rDNA. The taxa were chosen particularly to break up a long branch which appeared between *Gonatocerus* and the remainder of Chalcidoidea during preliminary analyses. The 'pteromalid lineage' is represented by five families in addition to Pteromalidae: Chalcididae, Eucharitidae, Eurytomidae, Perilampidae, and Torymidae. Although these families are not a comprehensive list of members of the 'pteromalid lineage,' constraints on the taxonomic size of the data set prevented the inclusion of additional taxa. Families were generally excluded because they represented very small clades (e.g., Leucospidae, Ormyridae) or they were too poorly defined to select appropriate exemplars (e.g., Agaonidae). Although Perilampidae represents a small number of taxa, it was included in the analysis because its relationship with Eucharitidae is well supported and could be used to evaluate the ability of the data set to recover known clades. Eurytomidae was

intended to be represented by two taxa: *Eurytoma* (Eurytominae) and *Heimbra* (Heimbrinae). However, the extraction of *Eurytoma* proved too poor for amplification, and time constraints prevented amplification from a second specimen. Within Pteromalidae, 14 subfamilies are represented by 31 genera, including two tribes of Colotrechninae, Eunotinae, and Diparinae, and three of Cleonyminae.

Gene Sampling

CAD is a multienzymatic protein, composed of carbamoyl-phosphate synthetase II (CPSase), aspartate transcarbamylase, and dihydro-orotase, that catalyses multiple steps in the *de novo* synthesis of pyrimidines. Moulton and Wiegmann (2004) used ~4kb of CAD (particularly the CPSase domain) to resolve relationships within eremoneuran Diptera. The trees they recovered were strongly concordant with dipteran phylogenies based on morphology and 28S rDNA. In this study, I sequenced 1719 bp of the CPSase domain, which corresponds roughly to the 5' end of Moulton and Wiegmann's 4kb fragment.

DDC catalyzes the conversion of tyrosine to dopamine, and of tryptophan to serotonin. In contrast to PEPCK, both synonymous and non-synonymous changes in DDC have proven useful for resolving relationships within and between families and superfamilies of Lepidoptera (Fang et al.1997, Friedlander et al. 1998, 2000). In this study I sequenced 708 bp of DDC, which lies approximately in the center of previously studied fragments.

Enolase catalyzes the conversion of 2-phosphoglycerate to phosphoenolpyruvate in the glycolytic pathway, and catalyzes the reverse reaction during gluconeogenesis. Enolase was judged to be more slowly evolving than PEPCK or DDC by Friedlander et al. (1992), and it has been recently utilized to resolve Lower-Mesozoic-aged relationships within curculionid beetles (Farrell et al. 2001, Sequeira and Farrell 2001). Two copies of enolase were discovered in beetles by Sequeira and Farrell (2001), but these were easily distinguishable by intron structure. Although only one copy amplified in most taxa in this study, two copies were found in a few. Intron structure could not be examined because the gene was amplified by RT-PCR, but the two copies within species were much more divergent from each other than from the apparently corresponding copies in other taxa. Thus, establishment of orthology was not problematic.

PEPCK and DDC were initially judged to be comparably intermediate in rate (Friedlander et al. 1992), but DDC has subsequently been shown to evolve much more rapidly. PEPCK catalyzes the conversion of oxaloacetate to phosphoenolpyruvate during gluconeogenesis. Non-synonymous changes in PEPCK recovered Mesozoic-aged subordinal divergences in Lepidoptera (Friedlander et al. 1996), but the amino acid sequence was largely invariant at lower taxonomic levels. In an application of ~500 bp of PEPCK to the phylogeny of Apidae: Xylocopinae (Leys et al. 2002), information occurred largely in the third codon position. In this study 1044 bp of PEPCK were sequenced, of which the Leys et al. and Friedlander et al. fragments correspond roughly to the 3' half.

Sample Collection and Storage

Most specimens were collected directly into 100% EtOH at room temperature and transferred within a month to storage at –80°C. Specimens collected in malaise traps in 95% EtOH proved satisfactory, as long as they were placed in 100% EtOH at –80°C within a month of collection. Vouchers for all taxa except *Alloterra sp.* (for which only a single specimen was collected) are stored at –80°C at the Center for Biosystems Research, University of Maryland Biotechnology Institute. Since extractions were conducted on entire specimens, voucher specimens represent individuals judged to be the same species based on morphological analysis and from the same collecting event.

Extraction and Amplification

Total nucleic acid (TNA) extractions were performed using an SV Total RNA Isolation System (Promega). Extractions were conducted on entire specimens, due to the minute size of these insects (most are <2mm). The extractions were subsequently lyophilyzed and rehydrated in a smaller volume (20 μl, 1/5 of initial volume) to concentrate the nucleic acids. All genes were amplified by RT-PCR to avoid introns. Reverse transcription was performed in 10μ of a solution including 2μl 25mM $MgCl_2$, 1μl 10X PCR buffer II (Applied Biosystems), 4μ 2.5mM dNTPs, 0.5μl RNase inhibitor (Applied Biosystems), 0.5μl RTase (Applied Biosystems), 1μl RC primer (20pm/μl), and 1μl of template. RT amplifications which used the general dT primer replaced the 1μl of specific primer with 0.5μl dT primer and 0.5μl H_2O. RT protocol was 42° for 35 min

followed by 99° for 5 min. Most of the RT steps used the reverse complement primer.

However, a general dT primer was used to amplify the enolase fragment 23F/344R,

because the RC primer preferentially amplified an undesired DNA fragment. PCR was

performed in a 50μl solution which included the 10μl solution from the RT Step, 2μl

25mM $MgCl_2$, 4μl 10X PCR buffer II (Applied Biosystems), 30.5μl H_2O, 0.5μl Taq

solution (1 part Amplitaq [5u/μl, Applied Biosystems] and 1 part TaqStart Ab [7μM,

Clonetech], 2μl F primer [20pm/μl], and 1μl RC primer [20pm/μl]. When the general dT

primer was used during the RT step, 1μl H_2O was replaced with 1 addtional μl of RC

primer. PCR protocol followed a touchdown method: 94° for 30 s, 24 cycles starting at

50° for 30 s and changing at –0.4° and +2 s/cycle, 94° for 30 s, 45° for 30 s, 12 cycles at

72° starting at 2 min and changing at +3 s/cycle, followed by 72° for 10 min. In the case

of DDC, enolase, and PEPCK, double stranded amplification products were isolated from

1.4% agarose gels. Primers were removed from CAD products were directly without gel

isolation, due to the lack of visible product produced in the RT-PCR phase. All

fragments were then reamplified using PCR and nested primers to both improve product

yield and ensure clean products. The reamplifications were done in a 50μl solution with

similar proportions to the PCR solution described in the RT-PCR step, and included 1μl

of the isolated RT-PCR products. Reamplication protocol was as follows: 94° for 30 s,

50° for 30 s, 21 cycles at 72° starting at 1 min and increasing +2 s/cycle, followed by 72°

for 10 min. All products were then gel isolated a second time. In cases where

concentration of the isolated product was high enough for sequencing, a second

reamplification was performed using M_{13} sequences added to the 5' end of all primers,

and these products were again gel isolated and purified.

Primer Developement

All primers are listed in Table 2. Primers with a C following the number are designed to be specific to Chalcidoidea, while the primer with an M following the number is designed to be specific to *Gonatocerus* (Mymaridae). CAD was amplified in two fragments: 46F/350RC reamplified with M_{13}REV/309RC and 295F/673RC reamplified with M_{13}REV/606RC. In cases where these steps resulted in no visible bands on agarose gels, various combinations of other listed primers were attempted (e.g. 46F/350RC reamplified with 61CF/ M_{13}(-21)). DDC was initially amplified using 1.7F/4RC. Nested PCR reamplification used M_{13}REV/3.3RC and 1.9CF/M_{13}(-21) (1.9F for outgroups) to produce two overlapping fragments. In taxa where the fragment was not amplified by this method, 1.6F was used in placed of 1.7F, and the nested reamps described above were used. Enolase was amplified in 2 fragments: 23F/344RC reamplified with M_{13}REV/241RC and 167F/407RC reamplified with M_{13}REV/406RC. For PEPCK, 2-3 fragments were amplified: 159CF/351RC (155F for outgroups) reamplified with M_{13}REV/335RC and 291F/510RC reamplified with 292F/ M_{13}(-21). In many cases 292F/510RC did not produce a clean band, and in these cases the RT-PCR product was reamplified using both 344CF/ M_{13}(-21) (344F for outgroups) and M_{13}REV/501RC to produce 2 overlapping fragments. *Gonatocerus* (Mymaridae) had a single amino acid insertion near the 501RC primer, which significantly altered its amino acid sequence through the primer region. A taxon-specific primer (501MRC) was developed specifically for this amplification.

Sequencing and Assembly

Products were isolated a final time and directly sequenced (both strands) from M$_{13}$ primers. Sequence chromatograms were checked for accuracy, and contigs were assembled using the software package Staden (Staden 1999). Alignments were straightforward due to sequence and length conservation, and were done manually in GDE (Smith et al 1994).

Phylogenetic Analysis

The data were partitioned by gene and codon position, and each partition was examined for base compositional homogeneity using the χ^2 test as implemented in PAUP* version 4 (Swofford 1999). All parsimony and likelihood analyses were conducted using PAUP* version 4 (Swofford 1999). Parsimony analyses were performed both on all nucleotides and on amino acids using equal weights and a heuristic search with 100 random addition replicates. Additionally, parsimony analyses were run using both individual genes and the combined data set. Maximum likelihood analyses were performed using a GTR+Γ+I model on both all nucleotides and nt1 and 2 only. The model was selected using a generalized likelihood ratio test with likelihoods calculated in PAUP* on a neighbor-joining tree from J-C, F81, HKY, GTR, GTR+Γ, GTR+I, and GTR+Γ+I models. Maximum likelihood analyses were performed as follows: 1) A starting tree was generated using the parsimony criterion and all nucleotides equally weighted. Only one of the most parsimonious trees was saved at this step. 2) Likelihood

parameters were estimated from the parsimony tree, and a likelihood analysis was

performed using the tree from step 1, the estimated parameters, and nearest-neighbor

interchange. 3) Likelihood parameters were estimated from the final step-2 tree, and this

tree and parameter set were used for a second likelihood analysis using tree bisection and

reconnection. 4) The final tree from step 3 was saved and its likelihood parameters were

estimated. 5) The likelihood parameters were set to those estimated in step 4, a heuristic

search with 100 random addition replicates and TBR branch swapping was performed,

and the most likely tree from step 5 was also saved. Two different types of searches

(steps 1-4 and 5) were performed in order to maximize the chance of actually finding the

most likely tree, although in all analyses the tree from step 4 topologically matched the

step 5 tree. Bootstrap values were calculated on the analysis of all nucleotides using a

GTR+Γ+I model with parameters set to those estimated in step 4, using 350 replicates

and 10 random addition sequences per replicate. Combinability of the individual gene

data sets was tested using the ILD test (Farris et al 1994) as implemented in PAUP*

version 4 (Swofford 1999) using the amino acid data set, as no preferred analysis

included equal weighting of synonomous and non-synonomous substitutions. The ILD

test was based on 100 replicates and 10 random addition sequences per replicate, and an

analysis was run for all genes and for all 2-gene combinations. Taxonomic groups which

were rendered paraphyletic in the phylogenetic analysis were tested against the null

hypothesis of monophyly using Shimodaira's approximately unbiased (AU) test (2002),

as implemented in the CONSEL package (Shimodaira and Hasegawa 2001). Constraint

trees used for the AU test were generated as in steps 1-4 above, except that in all searches

the group being tested was constrained as monophyletic.

Results

Characteristics of genes

As predicted, the four genes showed complementary rates of divergence. Pairwise comparisons across chalcidoids at second codon positions (nt2) showed that enolase evolves most slowly (0-3% uncorrected pairwise distance), followed by PEPCK (1-6%), DDC (0-9%), and CAD (2-13%) divergence. For all genes, nt3 showed moderate divergence across taxa within the same tribes (9-24% minimum uncorrected pairwise distances across genes) but appeared to approach saturation in more distant comparisons, with maximum pairwise divergences ranging from 66-76%. Base composition (Table 3) was homogenous across taxa at nt1 and nt2 for all genes. However, nt3 was significantly non-homogenous across taxa for all genes.

The ILD tests (Table 4) showed minimal evidence of discordant phylogenetic signal among genes. When all genes were analyzed together, homogeneity of signal was rejected at a modest level (p = 0.02). However, among the twelve pairwise combinations of genes, homogeneity was rejected, at modest levels (p = 0.02 – 0.05), only in the comparisons involving enolase.

Phylogeny estimation

Unweighted, unordered parsimony analyses of both all nucleotides and inferred amino acids yielded trees with little resolution or bootstrap support (results not shown).

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This discussion will therefore focus on the maximum likelihood analyses, which yielded more resolved trees with higher branch support.

In the best ML-score tree found for all nucleotides under the GTR+Γ+I model (Figure 70), 23 of 42 nodes have bootstrap support (BP) > 50%, of which 16 have BP > 70%. Monophyly of Chalcidoidea is supported (71% BP), as is the basal placement of Mymaridae (96% BP). *Encarsia* (Aphelinidae) branches off next (77% BP), in agreement with Campbell et al. (2000), followed by Eulophidae. The remaining families, all belonging to the 'pteromalid lineage,' form a monophyletic group, albeit with weak support.

The basal branches within the 'pteromalid lineage' are all subfamilies of Pteromalidae, namely, Herbertinae, Cerocephalinae, Spalangiinae, and Cleonyminae: Cleonymini. Pteromalidae, therefore, is paraphyletic with respect to all the other 'pteromalid lineage' families sampled, namely, Eurytomidae, Torymidae, Chalcididae, Eucharitidae, and Perilampidae. Chalcididae itself is recovered as monophyletic (95% BP). Some, but not all, relationships of individual families to sub-groups of Pteromalidae are strongly supported. A clade consisting of Eucharitidae plus Perilampidae (59% BP) is strongly grouped with Eutrichosomatinae (Pteromalidae) (82% BP). Both Eurytomidae and Torymidae fall (separately) within a moderately well supported clade consisting otherwise of the pteromalid groups Colotrechnini, Asaphinae, Pireninae and Coelocybinae. Monophyly of Pteromalidae is conclusively rejected overall by the approximately unbiased (AU) test of Shimodaira (2002; $p = 7 \times 10^{-15}$).

Within Pteromalidae, monophyly was nearly always strongly supported for tribes represented by multiple exemplars, including: Neapterolelapini (100% BP) and Diparini

(58% BP) of Diparinae; Lyscini (98% BP) of Cleonyminae; and Eunotini (100% BP)

and Moranilini (100% BP) of Eunotinae.   Monophyly of some subfamilies, e.g.,

Cerocephalinae (100% BP), was supported. A number of other subfamilies appeared

para- or polyphyletic in the tree, including Diparinae, Eunotinae, Ormocerinae,

Cleonyminae, and Colotrechninae, but support for these conclusions was generally weak.

In particular, one of the two taxa included from Ormocerinae, *Hemadas*, has sometimes

been placed within Pteromalidae without subfamily affiliation rather than within

Ormocerinae. The AU test significantly rejected monophyly only for Miscogasterinae (p

= 0.017) and Colotrechninae (p=.0002; see below).

A number of interesting relationships among pteromalid subfamilies (and other

families) are suggested by this analysis, although the deeper divergences are mostly

weakly supported. There is some support (59% BP) for a clade consisting of the entire

'pteromalid lineage' except Herbertinae and Cerocephalinae. There is moderate support

(73% BP) for a clade comprising Pteromalinae, Miscogasterinae, Colotrechnini

(Colotrechninae), Asaphinae, Eurytomidae, *Ganstrancistrus + Semiotellus*, Torymidae,

and Coelocybinae, and somewhat weaker support (63% BP) for a group including these

plus Diparinae, Lyscini (Cleonyminae), Hetreulophini (Colotrechninae) and Moranilini

(Eunotinae). Within this assemblage, Colotrechnini and Asaphinae are strongly

supported as sister groups (90% BP). Miscogasterinae and Pteromalinae form a clade

together (55% BP), though neither subfamily is monophyletic.

The ML tree using nt1 and 2 only based on a GTR+Γ+I model is shown in Figure

71. Clades marked with "*" were recovered in both analyses but with bootstrap support

<50% in the nt1+2 analysis. The topologies of this tree and the all-nts tree were highly

congruent at the tips and base of the phylogeny, and all nodes supported by >75% bootstrap support in the all-nts tree were resolved in the nt1+2 tree. Chalcidoidea was also resolved as monophyletic in both analyses, as was the clade Eutrichosomatinae + (Eucharitidae + Perilampidae). All con-tribal taxa were recovered in monophyletic clades in both analyses. The 'pteromalid lineage,' supported as monophyletic in the all-nts analysis, was monophyletic in the nt1+2 analysis with the exception of Torymidae. Torymidae changed positions drastically in the two analyses, moving from nested deep within Pteromalidae (in a clade supported with 73% BP) to the base of tree, positioned basally to Eulophidae. Herbertinae in particular was recovered as sister-group to Eulophidae, and Cleonymini retained a basal position in the complex. However, Spalangiinae and Cerocephalinae formed a clade deep with Pteromalidae rather than basally.

The large, moderately supported clade in the all-nts analysis loses a significant number of members, but the group appears to be united by a much longer branch. The clade retains the Pteromaline-Miscogasterine complex, which is sister group to *Heimbra* + (Colotrechnini + Asaphini), as it was resolved in the all-nts analysis. Torymidae, and the pteromalid subfamilies Pireninae and Coelocybinae are removed from the clade. The internal phylogeny of Diparini is identical in both analyses as *Lelaps* + (*Parurios* + (*Dipara* + *Alloterra*)).

Discussion

Chalcidoid and pteromalid phylogeny

The monophyly of Chalcidoidea is well supported in this analysis (71% BP for all-nucleotide ML, recovered in both analyses), corroborating previous morphological and molecular evidence. Previously, Gibson (1986) hypothesized Chalcidoidea to be monophyletic based on 3 morphological synapomorphies: 1) presence of multiporous plate sensillae on the antennal flagellum, 2) unique position of mesothoracic spiracle, and 3) prepectus visible externally. The basal position of Mymaridae, strongly supported here (96% BP for all-nucleotide ML, recovered in both analyses), also corroborates morphological evidence, including unique features of the ovipositor (Quicke et al. 1994) and thoracic musculature (Heraty et al. 1997). Additionally, Campbell et. al's (2000) analysis using 28S rDNA resolved Chalcidoidea as monophyletic and Mymaridae as the basal-most taxon, although without strong bootstrap support.

In Campbell et al's (2000) analysis, *Encarsia* (Aphelinidae) came out basal to all chalcids except for Mymaridae and a few other aphelinid genera. (Aphelinidae is most likely polyphyletic [Gibson et al. 1999], thus *Encarsia* is referred to here by its generic rather than family name). *Encarsia* was included in this analysis in an attempt to break up the long branch between the mymarid and the remaining chalcidoids, and was placed in that position with moderate support (77% BP in all-nts, recovered in both analyses). The congruence between this analysis and that of Campbell et al. (2000) in recovering

basal chalcidoid relationships that are well supported by morphology suggests that both

28S rDNA and protein-coding nuclear genes are useful at this deeper level.

The 'pteromalid lineage,' supported as monophyletic in the all-nts analysis, was

monophyletic in the nt1+2 analysis with the exception of Torymidae. The position of this

family differs drastically between the two trees and should be regarded as unsettled. The

decisive rejection of monophyly of Pteromalidae by the AU test suggests that

classification of the pteromalid lineage will need extensive revision, once relationships

are established in more detail than at present. Either the majority of other families in the

'pteromalid lineage,' including Eurytomidae, Chalcididae, Eucharitidae, Perilampidae,

and possibly Torymidae, should be classified as derived groups within Pteromalidae, or

Pteromalidae should be divided into multiple families.

Within the 'pteromalid lineage,' some morphologically-based groups which

appeared polyphyletic in the Campbell et al. (2000) analysis were well supported as

monophyletic in this analysis, including Eunotini (Eunotinae), Chalcididae, and

Eucharitidae + Perilampidae. The monophyly of *Eunotus* + *Scutellista* (Eunotini) was

strongly supported (100% BP in all-nts, recovered in both analyses), as was the

monophyly of *Hockeria* + *Dirhinus* (Chalcididae) (95% BP in all-nts, recovered in both

analyses). While Campbell et al. (2000) had a broader tribal-level sampling of

Chalcididae, none of the tribes were resolved as sister-taxa, including the two resolved as

monophyletic in this analysis (Dirhinae and Haltichellinae). The recovery of Chalcididae

as monophyletic in this analysis adds support for the ability of nuclear protein-coding

genes to recover chalcidoid relationships, as the group is strongly supported as

monophyletic by morphological evidence (Wijesekara 1997). Differences in taxa most

likely do not account for the difference in clade recovery between this analysis and that of Campbell et al. (2000), as identical genera of Eunotini and Chalcididae were sampled in both groups.

Although Boucek (1988) considered Eutrichosomatinae to be one of the most primitive members of Pteromalidae, no hypotheses have been put forth regarding its sister-group relationships. Monophyly of the Eucharitidae + Perilampidae is supported by morphological evidence, primarily characteristics of their planidiaform larvae (Heraty and Darling 1984). Campbell et al.'s (2000) study of 28S rRNA did not support this clade as monophyletic. The present analysis supports the monophyly of Perilampidae + Eucharitidae (59% BP in all-nts, recovered in both analyses), and strongly supports the monophyly of Eutrichosomatinae + (Perilampidae + Eucharitidae) (82% BP in all-nts, recovered in both analyses).

One large pteromalid clade which is supported as monophyletic in both analyses is (Pteromalinae, Miscogasterinae) + (*Heimbra* + (Colotrechinae: Colotrechnini + Asaphinae)). The AU test results showed that while monophyly of Pteromalinae was not significantly less likely than non-monophyly, the monophyly of Miscogasterinae was significantly less likely ($p<0.05$). This suggests that even if the two do not truly render each other paraphyletic as suggested by the tree, minimally Pteromalinae renders Miscogasterinae paraphyletic. It should be noted that the two representatives of Miscogasterinae belong to different tribes, *Polstonia* belonging to Sphegigasterini and *Plutothrix* to Trigondonerini, suggesting that Trigodonerini may represent the basal lineage of the complex with Sphegigasterini derived from Miscogasterinae. A novel finding in this study is the strongly supported sister-group relationship between

Colotrechnus (Colotrechini) and *Enogerra* (Asaphinae) (90% BP in all-nts, recovered in both analyses). A close relationship with these two groups has never been proposed, and no morphological characters have been recorded to unite them.

Four subfamilies of pteromalids appeared to be polyphyletic in these analyses. Monophyly of Colotrechninae was strongly rejected (p<0.001) by the AU test. Colotrechninae is morphologically defined by the advanced placement and sculpture of the axillae, and this analysis suggests that these characters are independently derived in the two represented colotrechnine tribes, Colotrechnini and Hetreulophini. Tribes of Diparinae, Eunotinae, and Cleonyminae were strongly recovered as monophyletic, but like Colotrechninae were recovered as polyphyletic at the subfamily level. However, when subjected to the AU test, monophyly of Diparinae, Eunotinae, and Cleonyminae was not significantly less likely than non-monophyly. Gibson's (2003) morphological phylogenetic analysis of Cleonyminae produced similar results, as he could neither support its monophyly nor find a group that assuredly rendered it paraphyletic.

The phylogeny of Diparinae was studied using morphological characters (Desjardins, in prep), and monophyly of the group was strongly supported. As previously mentioned, while Diparinae was not recovered as monophyletic in this analysis, its monophyly was not rejected. Desjardins (in prep) also divided the subfamily into 2 tribes, Diparini and Neapterolelapini. The phylogenetic analysis here supports this split, as both tribes are recovered as monophyletic in the analysis. Additonally, the basal position of *Lelaps* with respect to *Dipara*, *Alloterra*, and *Parurios* is supported in both morphological and molecular analyses.

While not providing a phylogeny with robust support at all levels, nuclear

protein-coding gene data has provided a more well-supported hypothesis about the

phylogeny of Chalicidoidea, and particularly the 'pteromalid lineage,' than other

attempts. These genes proved superior to 28S rDNA in resolving monophyly of groups

that were well supported by morphological evidence, and both basal and tip clades within

Chalicidoidea were well supported. The many short internal branches of the phylogeny

are likely the result of an explosive and rapid diversification within the superfamily, and

the addition of new nuclear protein-coding gene data should expand phylogenetic

resolution into these areas of the phylogeny.

Evolution of life histories

The phylogenetic relationships hypothesized here permit re-examination of

several long-standing hypotheses about the evolution of different types of parasitism in

Chalcidoidea. Parasitism of wood-boring beetles has long been thought to be the

ancestral trophic habit of chalcidoids, presumably because the symphytan family

Orussidae, the sister-group to all parasitic Hymenoptera, also has this life history trait.

Additionally, many other parasitoid groups typically viewed as primitive (e.g.,

Proctotrupoidea) also parasitize wood-boring beetles. However, the basal position of

Mymaridae and *Encarsia* in this analysis provides evidence against the hypothesis that

wood-boring beetle parastism is ancestral within Chalcidoidea. While mymarids are egg

parasitoids, *Encarsia* parasitizes scale insects and whiteflies. Additionally, the first

wood-boring beetle parasitoid to appear within Chalcidoidea is Cerocephalinae, which

appears 4 nodes up from the node uniting Chalcidoidea. An explanation that parasitism of insects other than wood-boring beetles was derived independently in Mymaridae, Aphelinidae, Eulophidae, and possibly Herbertinae (Pteromalidae) from an ancestor which pararasitized wood-boring beetles is highly unparsimonious.

The implications for egg parasitism from this study are ambiguous, as within this phylogenetic context it appears to be an apomorphic biology of Mymaridae. It is possible that the ancestral chalcidoid started as an egg parasitoid and moved on to scale insects, which are similary small and immobile hosts. Knowledge of the sister-taxa to Chalcidoidea and their biologies might provide evidence to support this hypothesis. Mymarommatoidea is a rare superfamily (although common in the fossil record) which was hypothesized by Gibson (1986) to be sister-group to Chalcidoidea based on 3 unique characteristics of internal morphology. The hosts of Mymarommatoidea are unknown, but the extremely small size of these insects suggests that egg parasitism is likely. The sister-group to Mymarommatoidea is largely unknown. Some analyses by Dowton and Austin (1994, 1997) suggest that Platygastroidea may the sister-group of this clade, although they did not appear so in all analyses. As Platygasteridae is composed entirely of egg parasitoids, a sister group relationship between Platygastroidea and Mymarommatoidea + Chalcidoidea would add additional support to the anscestral state of egg parasitism within Chalcidoidea.

Regardless, these phylogenetic results suggest evolutionary trends opposite of what has typically thought to have occurred within Chalcidoidea. The large, robust bodied wood-boring beetle parasites (e.g., many cleonymine pteromalids) are obviously derived within Chalcidoidea, while small bodied parasitoids of immobile hosts are more

basal. Groups such as Mymaridae are thought of as highly reduced within Chalcidoidea.

However, the molecular data suggest that groups such Cleonyminae have

morphologically "expanded" from smaller and simpler body form. Within the

'pteromalid lineage,' however, it is likely that wood-boring beetle parastism is ancestral.

The groups which appear to occupy basal positions within this lineage, such as

Cerocephalinae and *Cleonymus* (Cleonyminae), typically possess this biology.

The sister-group relationship between Eutrichosomatinae (Pteromalidae) and

Eucharitidae + Perlilampidae is also biologically interesting. Although not sampled in

this analysis, morphological evidence for Chrysolampinae (classified in either

Perilampidae or Eucharitidae) supports its placement as sister-group to Perilampidae +

Eucharitidae (Heraty and Darling 1984), and it would likely be derived in this clade

relative to Eutrichosomatinae. Both Chrysolampinae and Eutrichosomatinae are primary

parasitoids of Coleoptera in flowering plants (Boucek 1974, Darling and Miller 1991,

Darling 1997). As both Eucharitidae and Perilampidae lay their planidiaform larvae in

flower heads, this suggests that their anscestor may have provided an environment for the

evolution of a planidiaform larva. Future studies of the Eucharitidae + Perilampidae

clade should include Eutrichosomatinae as an outgroup.

Table 1. Taxa sampled in this study, and their higher classification within Hymenoptera.

Higher Taxon	Genus	Higher Taxon	Genus
Ceraphronoidea		Eutrichosoma-tinae	*Eutrichosoma sp.*
Ceraphronidae	*Genus indet.*	Herbertiinae	*Herbertia sp.*
Chalcidoidea			*Plutothrix sp.*
Chalcididae		Miscogasterinae	
Dirhinae	*Dirhinus sp.*		*Polstonia sp.*
Haltichellinae	*Hockeria sp.*	Ormocerinae	*Hemadas sp.*
Encyrtidae	*Encarsia sp.*		*Semiotellus sp.*
Eucharitidae	*Kapala sp.*	Pireninae	*Gastrancistrus sp.*
Eulophidae	*Tetrastichus sp.*		
Eurytomidae	*Heimbra opaca*	Pteromalinae	*Brachycaudonia sp.*
Mymaridae	*Gonatocerus sp.*		
Perilampidae	*Steffanolampus sp.*		*Psilocera sp.*
Pteromalidae		Spalangiinae	*Spalangia cameroni*
Asaphinae	*Enoggera sp.*	Torymidae	*Torymus sp.*
Cerocephalinae	*Neocalosoter sp.*	Platygastroidea	
	Theocolax sp.	Platygasteridae	*Genus indet.*
Cleonyminae		Scelionidae	*Genus indet.*
Chalcedectini	*Chalcedectus sp.*		
Cleonymini	*Cleonymus sp.*		
Lyiscini	*Epistenia sp.*		
	Thaumasura sp.		
Coelycobinae	*Ormyromorpha sp.*		
Colotrechninae			
Colotrechnini	*Colotrechnus sp.*		
	Hetreulophus sp.		
Hetreulophini			
Diparinae	*Australolaelaps sp.*		
	Neapterolelaps sp.		
	Alloterra sp.		
	Dipara sp.		
	Lelaps sp.		
	Parurios sp.		
Eunotinae			
Eunotini	*Eunotus sp.*		
	Scutellista sp.		
Moranilini	*Moranila sp.*		
	Ophelosia sp.		

Table 2. Primers used in this study. F denotes a forward primer, RC denotes the reverse complement sequence of a reverse primer. Primers labeled with C are specific to Chalcidoidea, while the primer labeled with M specific to *Gonatocerus* (Mymaridae).

Gene	Primer Name	Primer Sequence (5' to 3')
CAD	46F	GTN GTN TTY CAR CAN GGN ATG GT
	61CF	GAY CCN TCN TAY TGY GAR CAR AT
	295F	TAY GGY AAY MGN GGN CAY AA
	309RC	CAR AAY CAY GGN TTY GCN GTN GA
	309CF	CAR AAY CAY GGN TTY GCN ATH GA
	350RC	CAR TTY CAY CCN GAR CAY
	606RC	TGG AAR GAR RTN GAR TAY GAR GTN GT
	673RC	GAR TGY AAY RTN CAR TAY GC
DDC	1.6F	TTY CAY GCN TAY TTY CC
	1.7F	GCH TGY ATY GGN TTY WCN TGG AT
	1.9F	ATG HTN GAY TGG YTV GGY CAR ATG
	1.9CF	ATG YTN GAY TGG YTN GGN AAR ATG
	3.3RC	TTY AAY TTY AAY CCN CAY AAR TGG
	4RC	GAY TAY MGD CAY TGG CAR ATH CC
Enolase	23F	AAY CCN ACN GTN GAR GT
	167F	GCN ATG CAR GAR TTY ATG
	241RC	ATH GGN ATG GAY GTN GC
	344RC	AAR GTN AAY CAR ATH GG
	406RC	GCN AAR TAY AAY CAR
	407RC	AAR TAY AAY CAR HTN YTN CGN ATH GAR GA
PEPCK	155F	CGN TTC CCN GGN TGY ATG
	159CF	TGY ATG AAR GGN CGN ACN
	291F	GAR GGN TGG YTN GCN GAR CA
	292F	GAR GGN TGG YTN GCN GAR CAY ATG
	344F/335RC	GAY GAY ATH GCN TGG ATG ARR TT
	344CF	GAY GAY ATH GCN TGG ATG CGN TT
	351RC	ATH AAY CCN GAR AAY GGN TTY TTY GG
	501RC	ATG CAY GAY CCN TTY GCN ATG
	501CRC	ATG AAY GAY CCN TTY GCN ATG
	501MRC	CAY GAY CCN TTY GCA ATG
	510RC	TTY TTY GGN TAY AAY TTY GG

Table 3. Base composition partitioned by gene and codon position. P-values are listed for the χ^2 test against a null hypothesis of base composition homogeneity across taxa.

gene	codon position	A	C	G	T	χ^2 p-value
pepck	nt1	0.30	0.20	0.35	0.15	1.00
	nt2	0.26	0.26	0.22	0.26	1.00
	nt3	0.16	0.37	0.27	0.20	<0.001*
ddc	nt1	0.24	0.19	0.37	0.20	1.00
	nt2	0.31	0.22	0.19	0.28	1.00
	nt3	0.28	0.22	0.20	0.30	<0.001*
enolase	nt1	0.32	0.15	0.38	0.15	1.00
	nt2	0.34	0.25	0.14	0.27	1.00
	nt3	0.19	0.31	0.20	0.30	<0.001*
cad	nt1	0.28	0.23	0.32	0.17	0.72
	nt2	0.32	0.23	0.18	0.27	1.00
	nt3	0.19	0.30	0.27	0.24	<0.001*

Table 4. P-values for pairwise comparisons of gene combinability using the ILD test. When all genes were included, the null hypothesis of homogeneity was rejected at the 0.05 level (p = 0.02).

	DDC	Enolase	CAD
PEPCK	0.08	0.03*	0.28
DDC	-	0.05*	0.07
Enolase	-	-	0.02*

Table 5. P-values from the A.U. test of non-monophyly. Taxonomic groups which did not appear monophyletic in the ML tree were subjected to the test.

taxonomic group	p-value
Eunotinae	0.412
Pteromalinae	0.376
Diparinae	0.225
Cleonyminae	0.143
Miscogasterinae	0.017
Colotrechninae	2×10^{-4}
Pteromalidae	7×10^{-15}
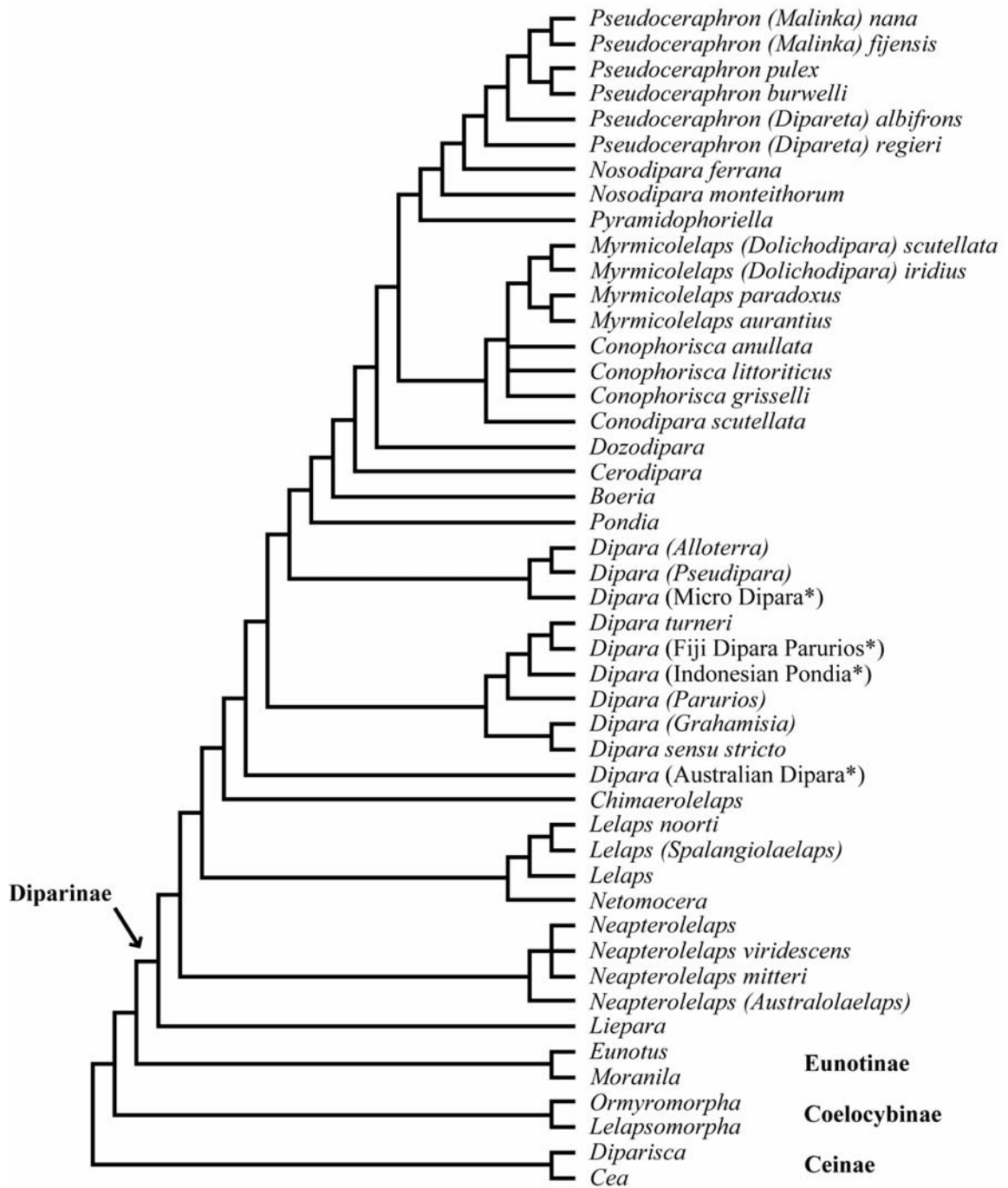
Figure 1. Preferred phylogenetic hypothesis. Maximum parsimony tree based on successive approximations of the data set excluding *Bohpa* but including bristle positional characters. Names in "()" refer to the classification of the taxon prior to this study. Names followed by "*" refer to units in the phylogenetic analysis, and do not represent valid names.
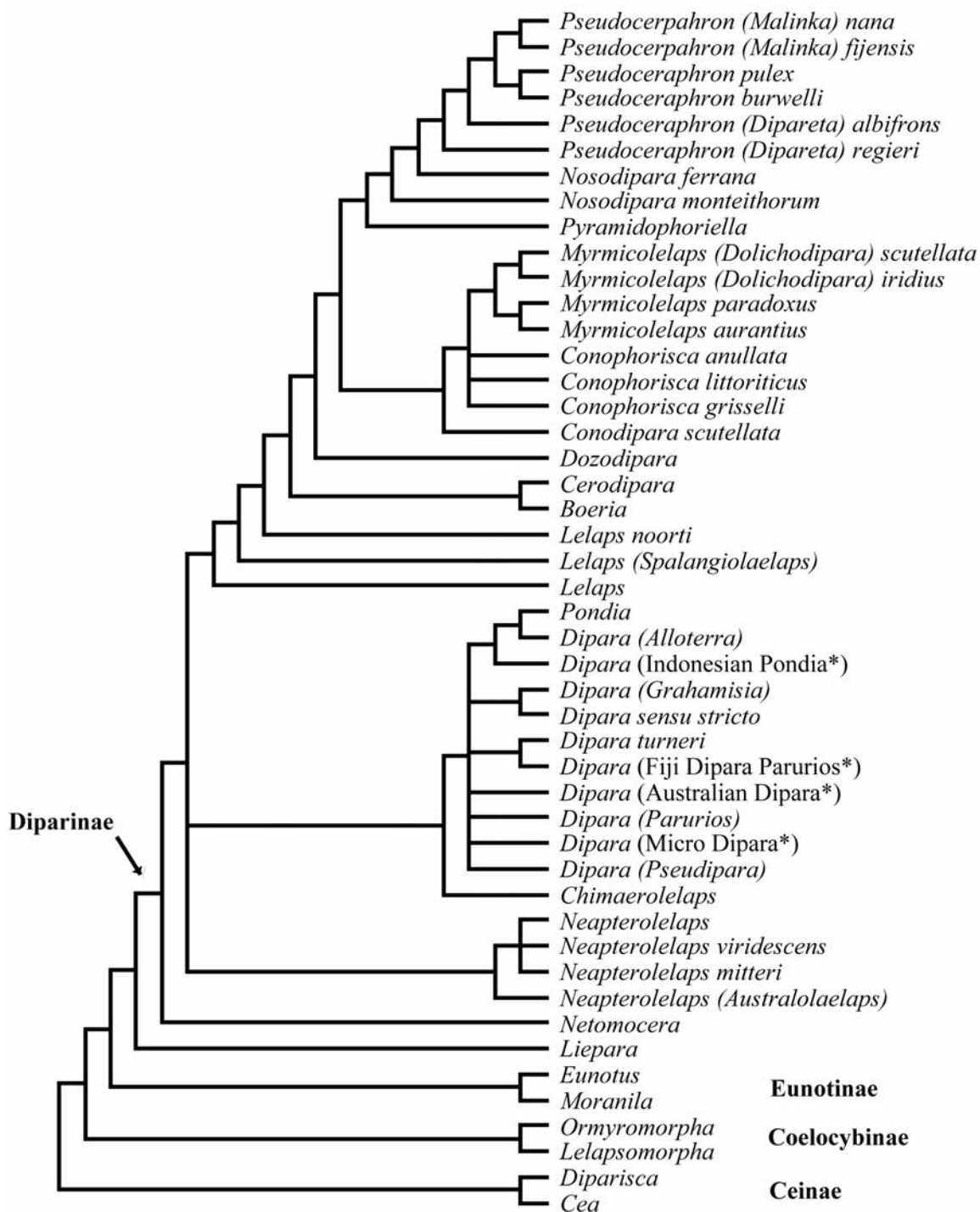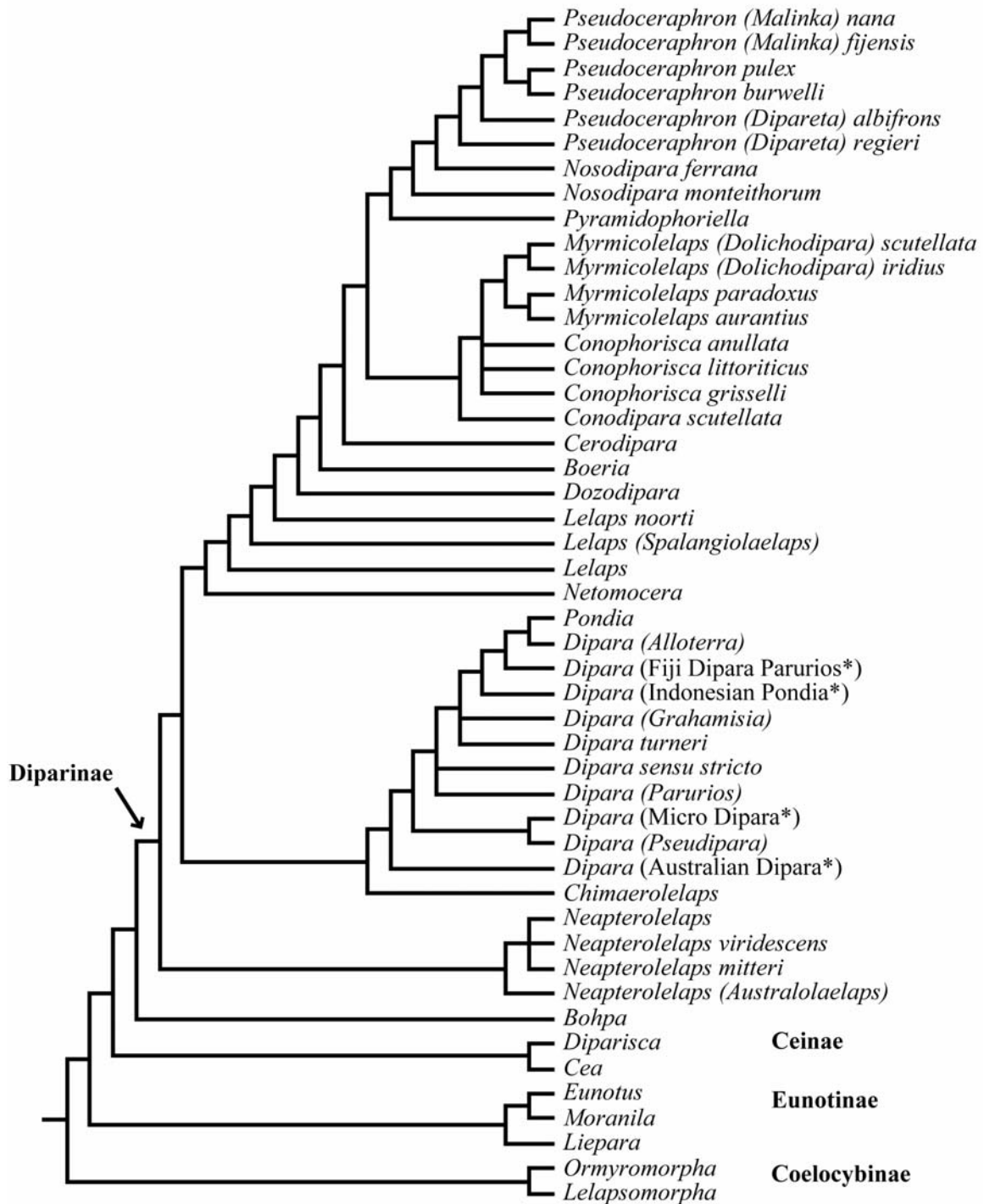
Figure 2. Maximum parsimony tree based on successive approximations of the data set excluding both *Bohpa* and bristle positional characters. Names in "()" refer to the classification of the taxon prior to this study. Names followed by "*" refer to units in the phylogenetic analysis, and do not represent valid names.

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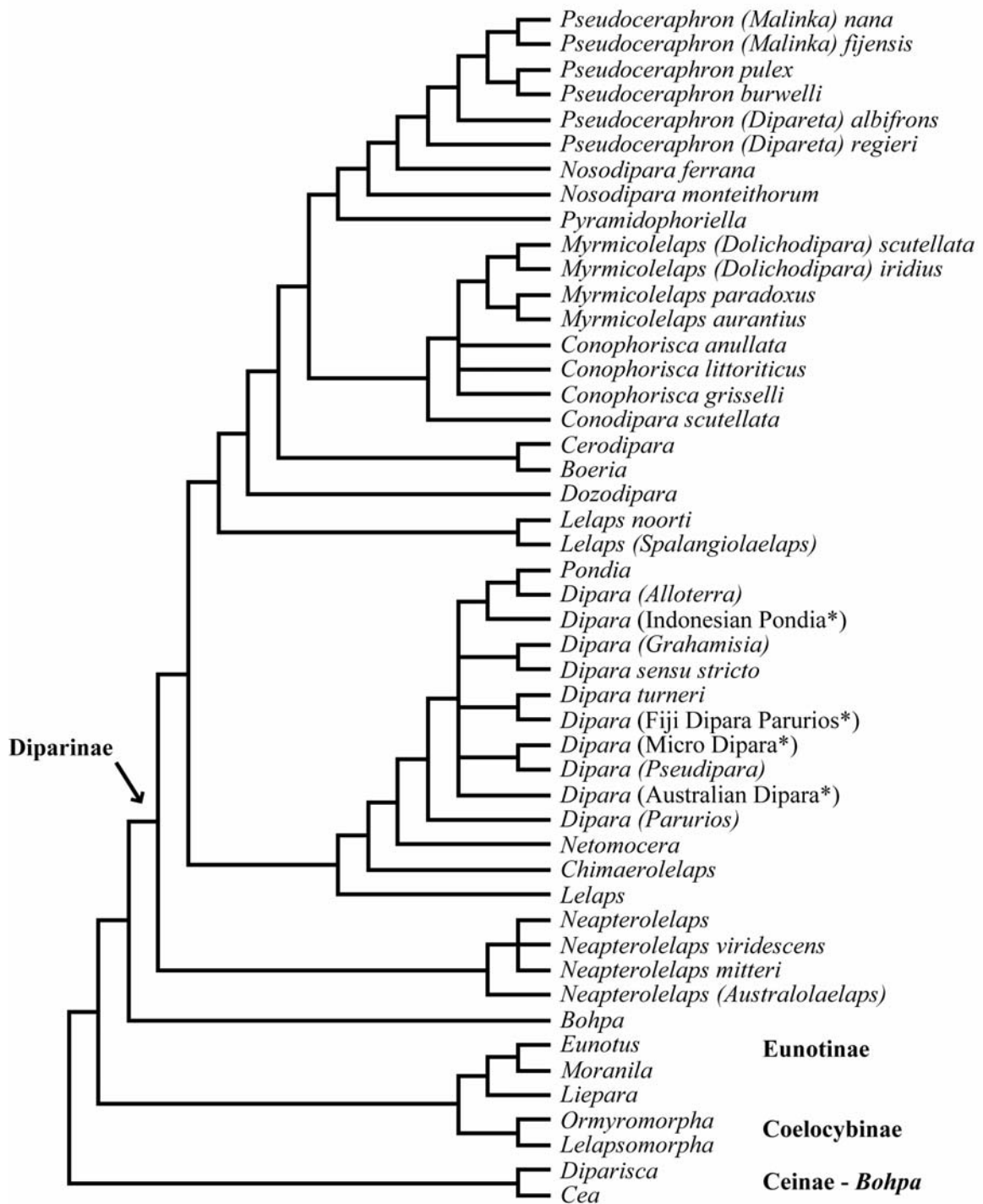
Figure 3. Maximum parsimony tree based on successive approximations of the data set including *Bohpa* but excluding bristle positional characters. Names in "()" refer to the classification of the taxon prior to this study. Names followed by "*" refer to units in the phylogenetic analysis, and do not represent valid names.

Figure 4. Maximum parsimony tree based on successive approximations of the data set including both *Bohpa* and bristle positional characters. Names in "()" refer to the classification of the taxon prior to this study. Names followed by "*" refer to units in the phylogenetic analysis, and do not represent valid names.
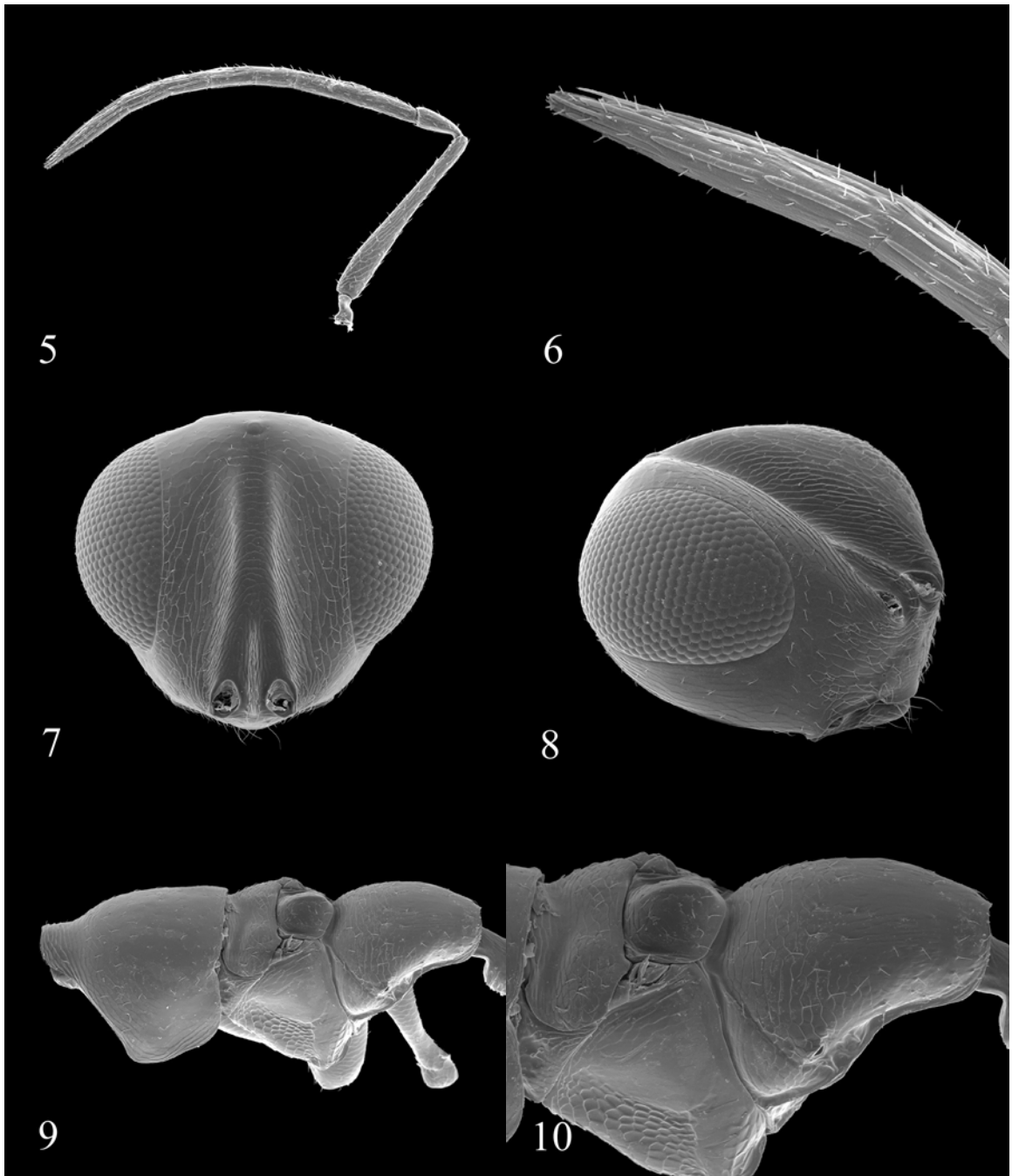
Figures 5-10. *Conophorisca grisselli*: 5, antenna; 6, clava; 7, head (frontal view); 8, head (ventro-latero-frontal view); 9, mesosoma (dorso-lateral view); 10, mesosoma - pronotum (dorso-lateral view).
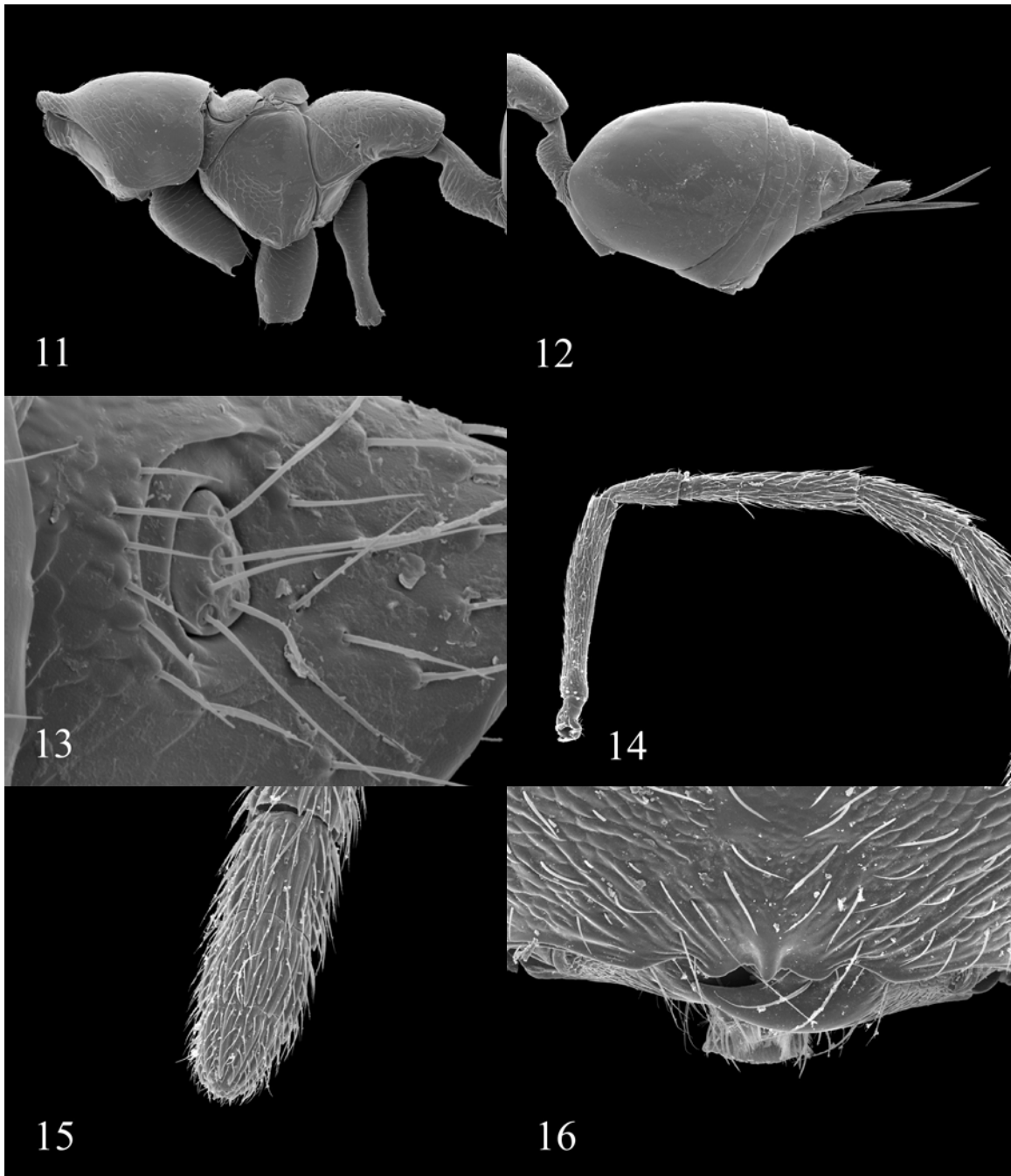
Figures 11-16. *Conophorisca grisselli*: 11, mesosoma (lateral view); 12, metasoma (lateral view); 13, cercus. *Lelaps sp. A*: 14, antenna; 15, clava; 16, clypeus.
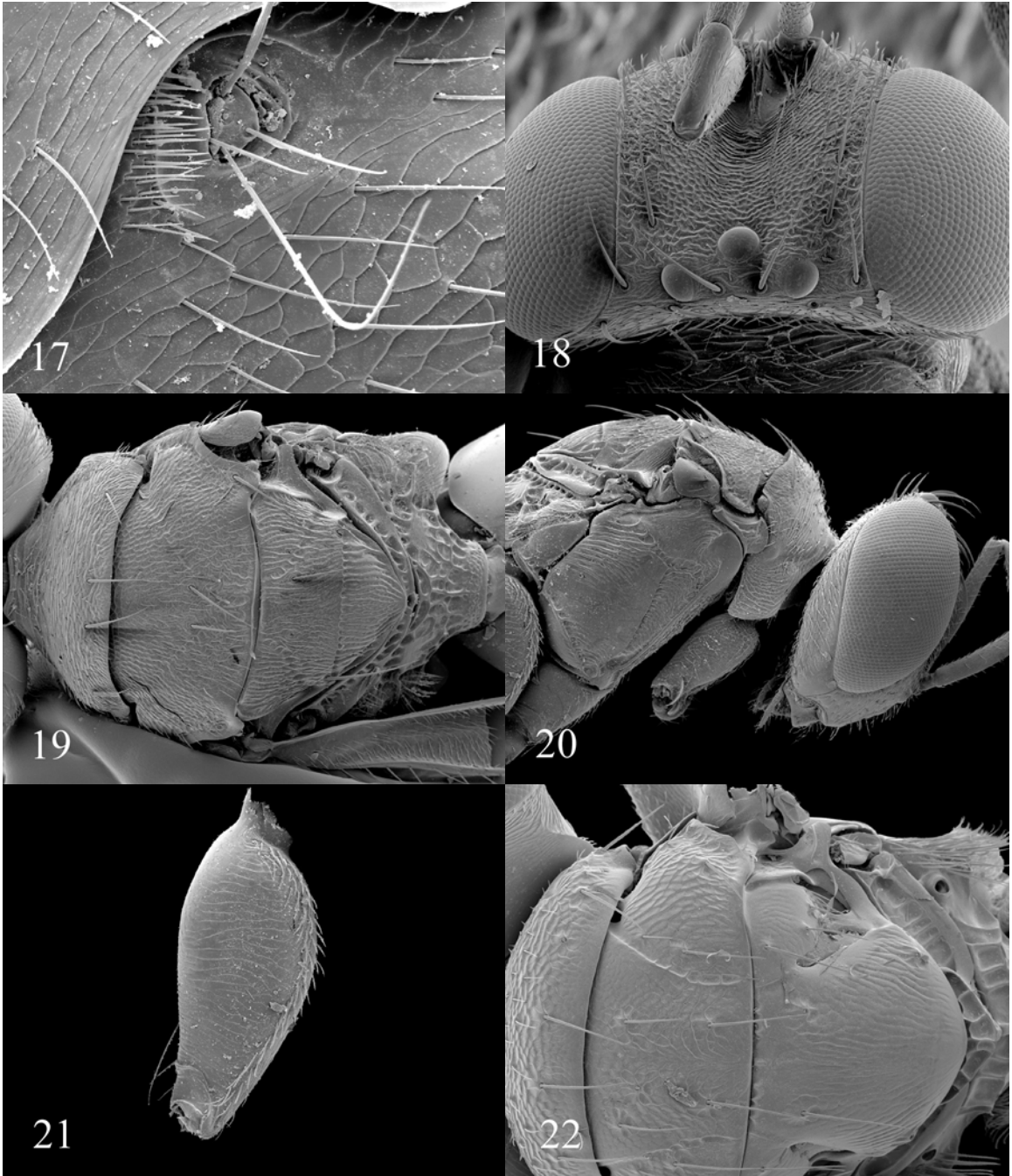
Figures 17-22. *Lelaps sp. A*: 17, cercus. *Lelaps sp. B*: 18, head (dorsal view); 19, mesosoma (dorsal view); 20, mesosoma (lateral view); 21, metacoxa. *Moranila sp.*: 22, mesosoma (dorsal view).
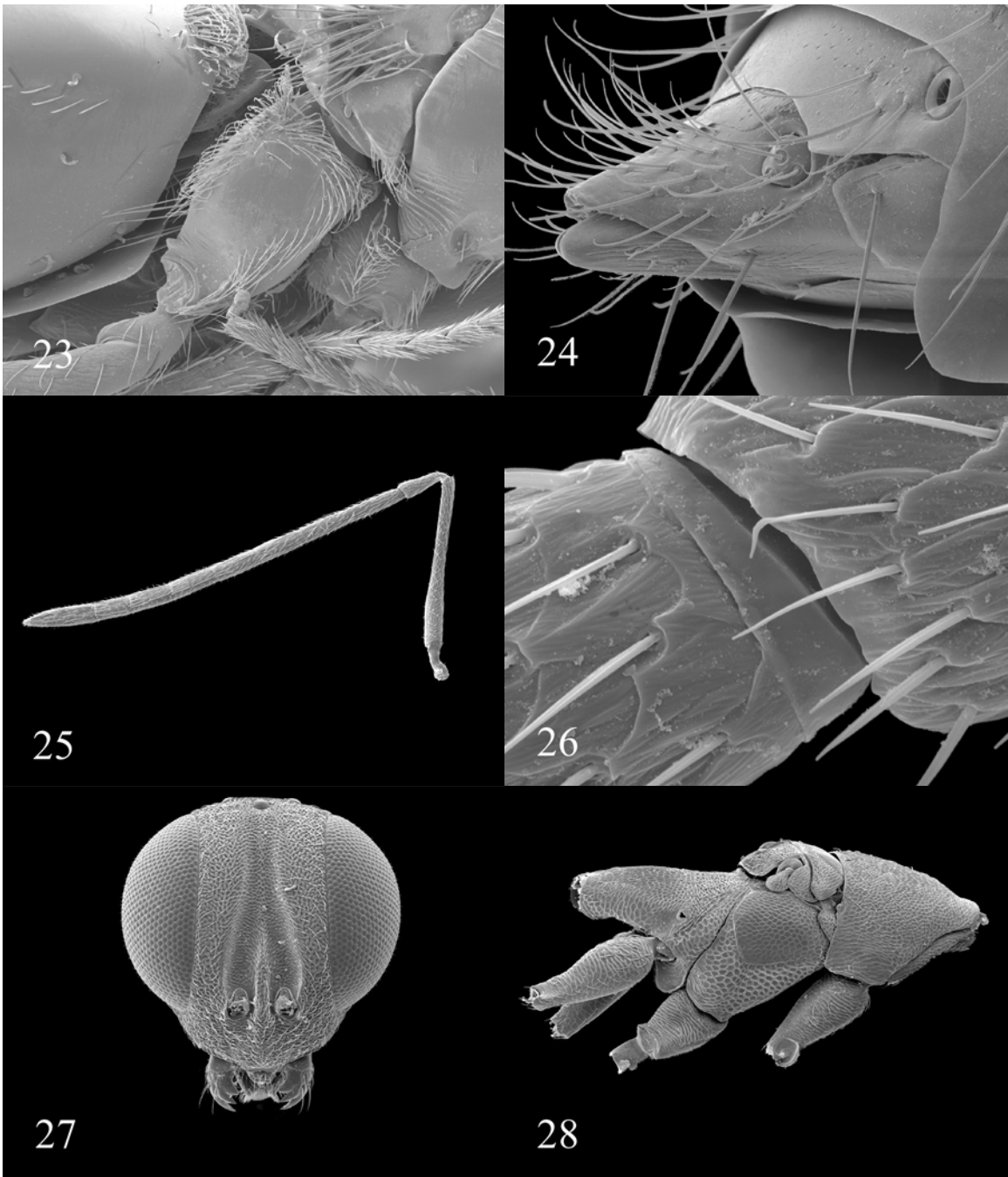
Figures 23-28. *Moranila sp.*: 23, metacoxa (lateral view); 24, cercus. *Myrmicolelaps aurantius*: 25, antenna; 26, anellus; 27, head (frontal view); 28, mesosoma (lateral view).
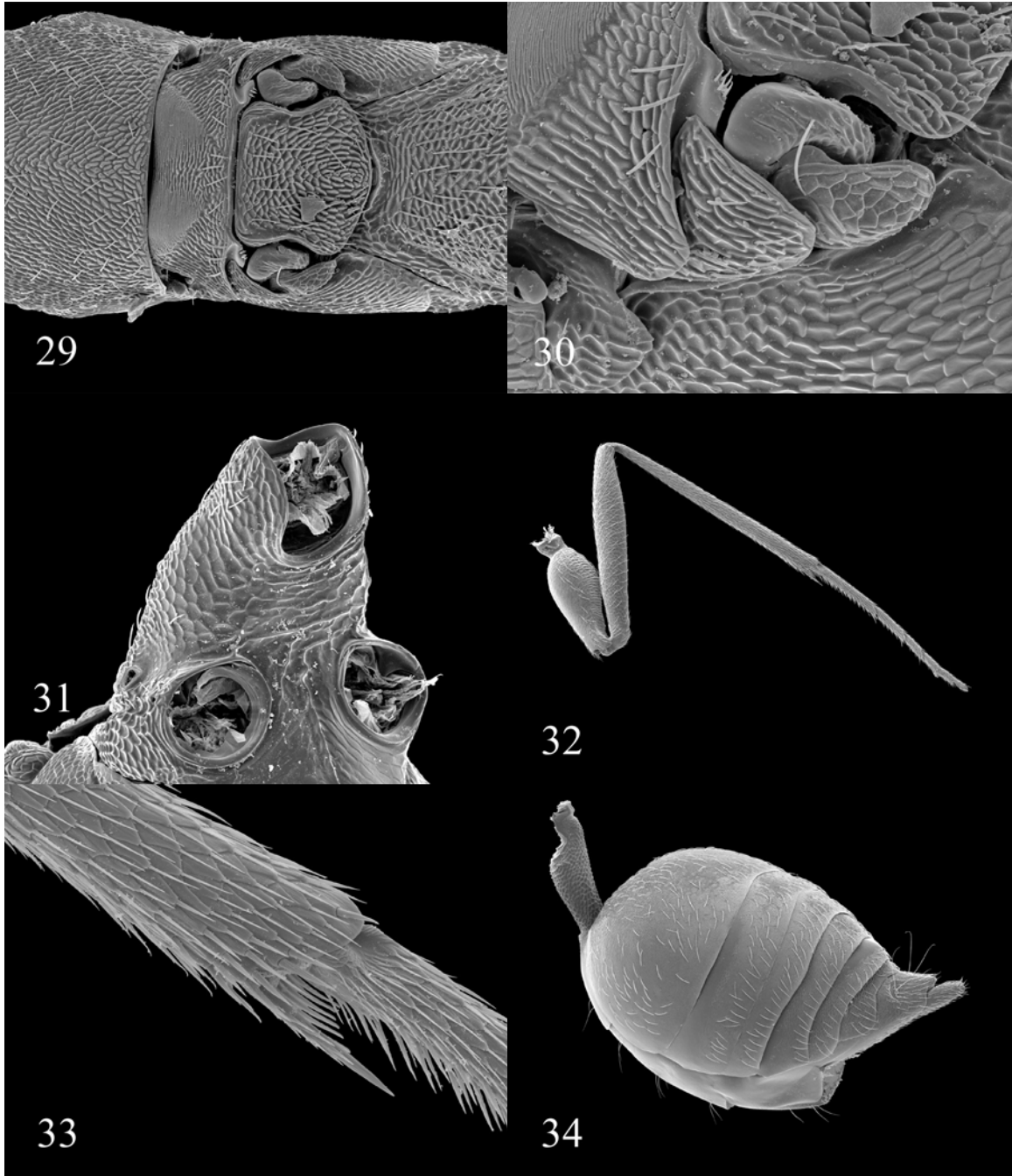
Figures 29-34. *Myrmicolelaps aurantius*: 29, scutum + scutellum (dorsal view); 30, scutellum (dorso-lateral view); 31, propodeal foramen + metasternum (posterior view); 32, metaleg; 33, metatibial spur; 34, metasoma (lateral view).
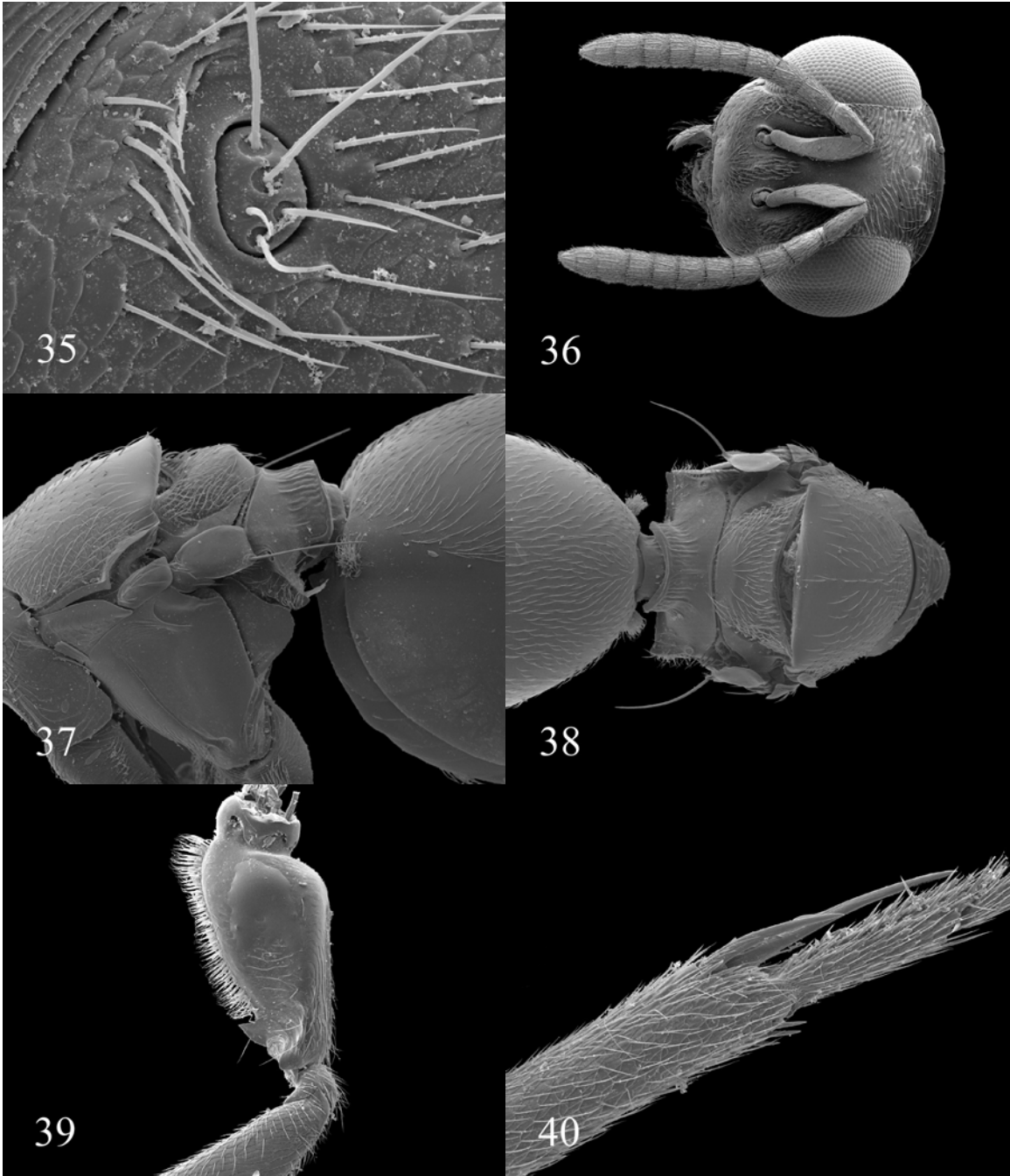
Figures 35- 40. *Myrmicolelaps aurantius*: 35, cercus. *Neapterolelaps sp.*: 36, head (frontal view); 37, mesosoma (lateral view); 38, mesosoma (dorso-posterior view); 39, metacoxa (lateral view); 40, metatibial spur.
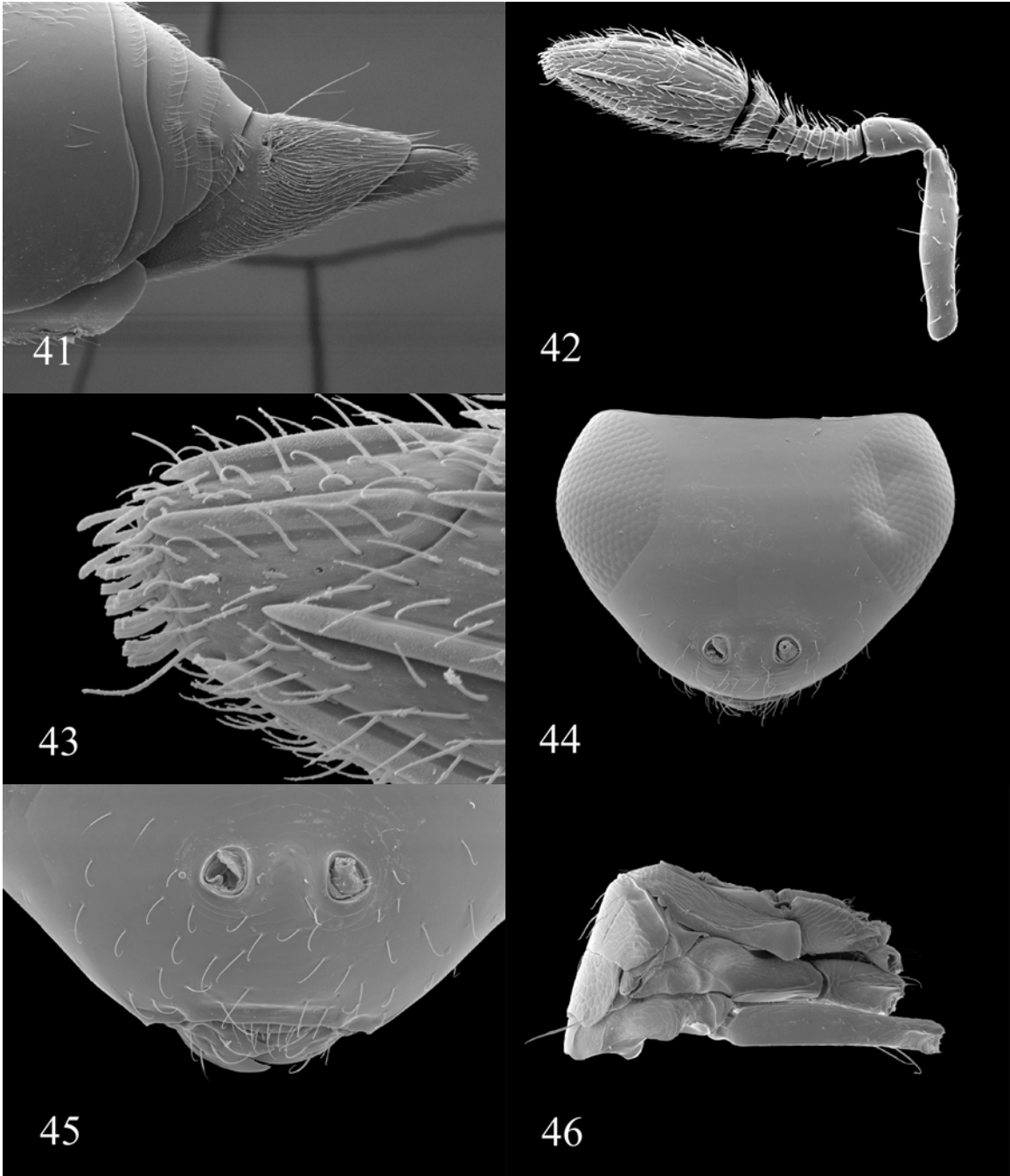
Figures 41-46. *Neapterolelaps sp.*: 41, cercus. *Pseudoceraphron burwelli*: 42, antenna; 43, clava; 44, head (frontal view); 45, clypeus; 46, mesosoma including coxae (lateral view).
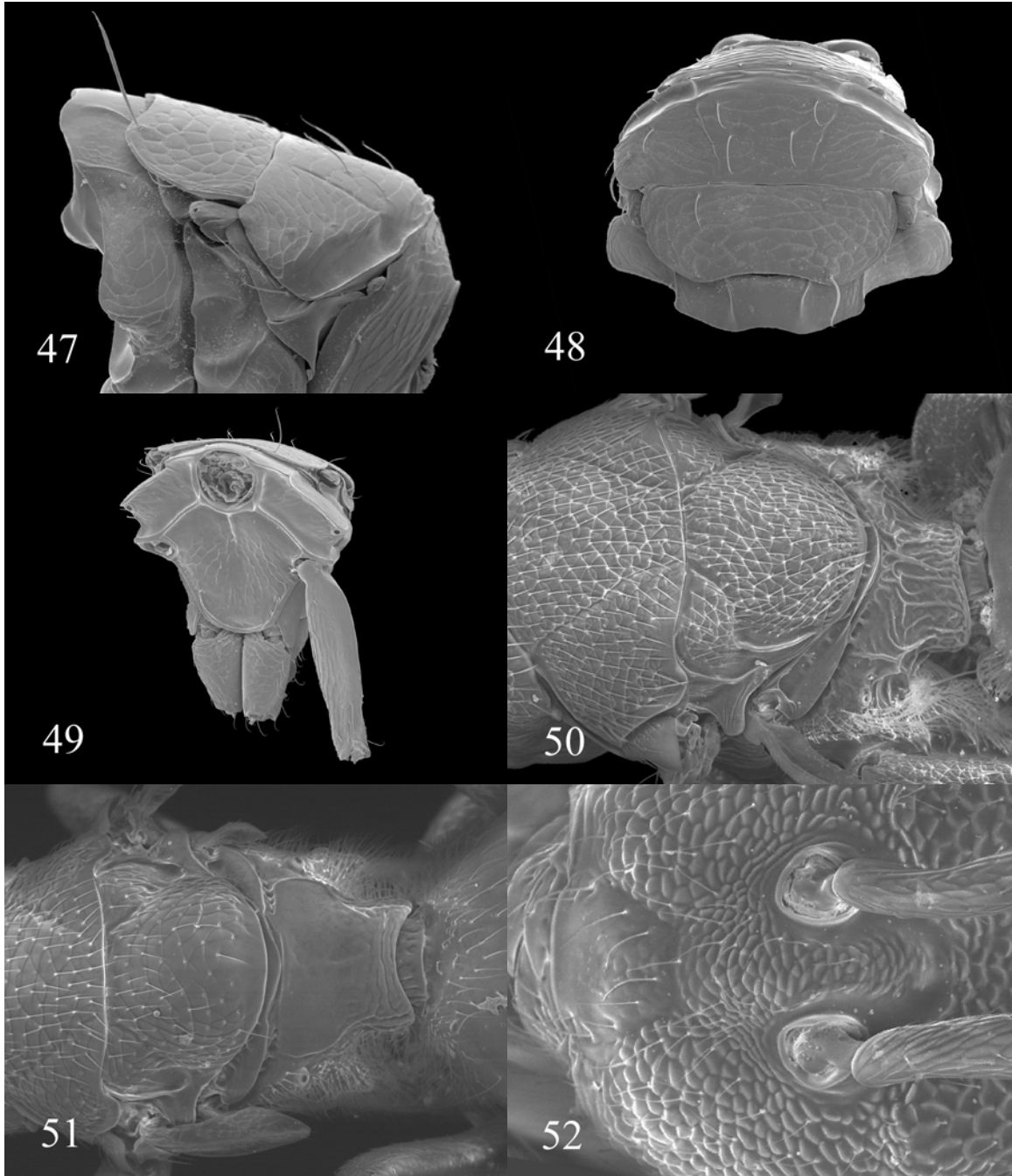
Figures 47-52. *Pseudoceraphron burwelli*: 47, mesosoma excluding coxae (lateral view); 48, mesosoma (dorsal view); 49, propodeum + metasternum (posterior view). *Neapterolelaps viridescens*: 50, mesosoma (dorso-lateral view). *Neapterolelaps mitteri*: 51, mesosoma (dorso-lateral view). *Pondia sp.*: 52, scrobe.
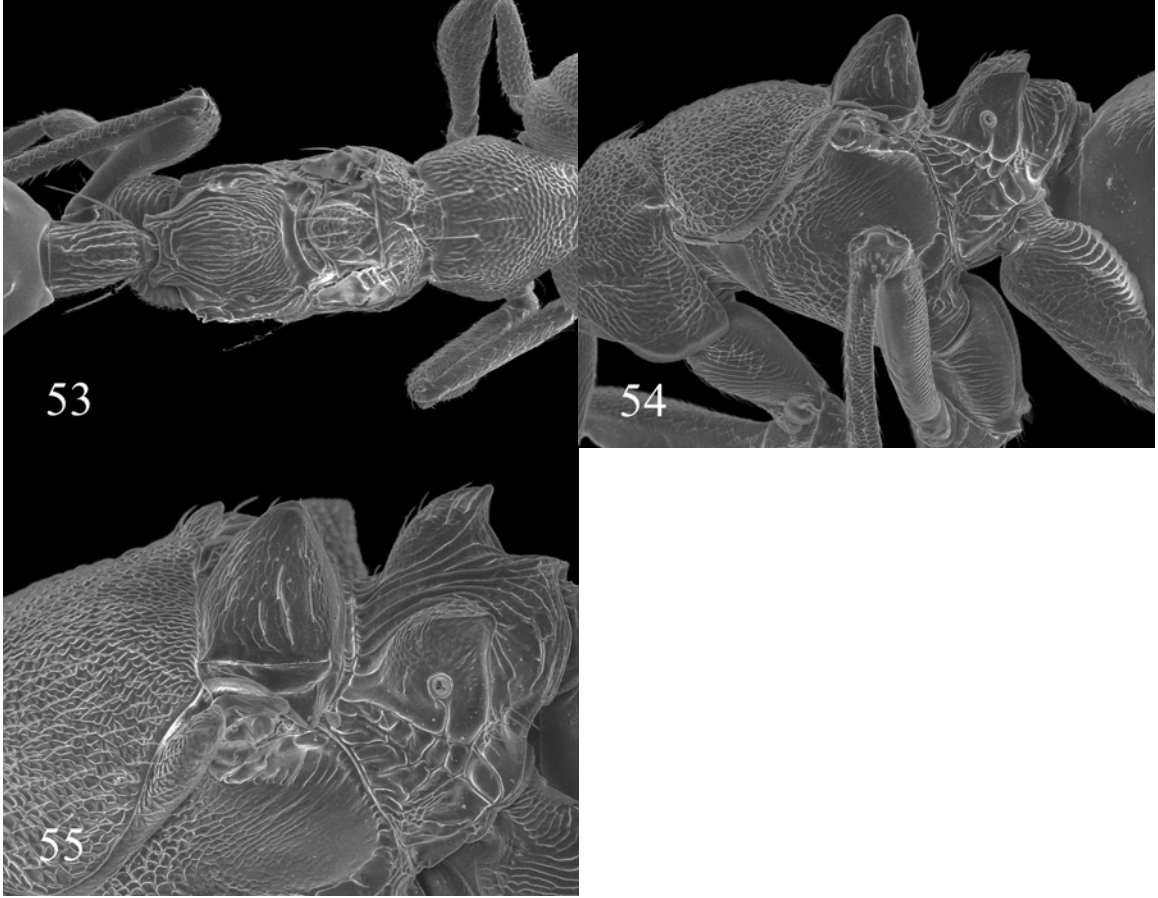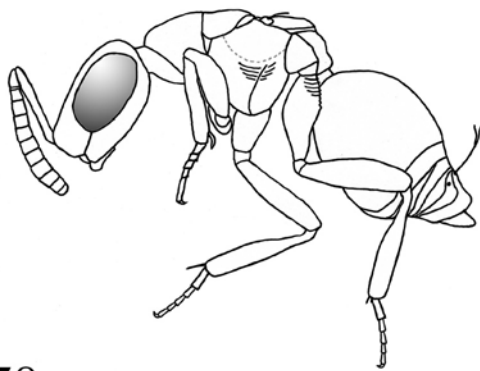
Figures 53-55. *Pondia sp.*: 53, mesosoma (dorsal view). *Pyramidophoriella sp.*: 54, mesosoma (lateral view); 55, mesosoma (dorso-lateral view).
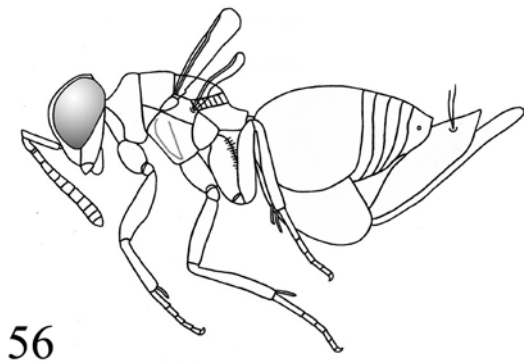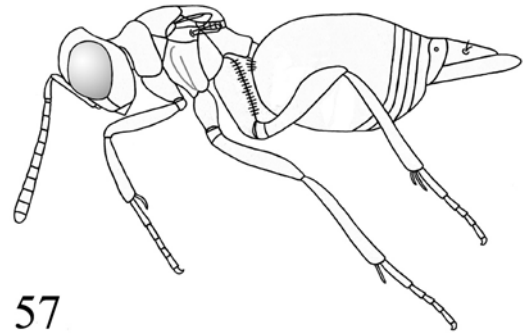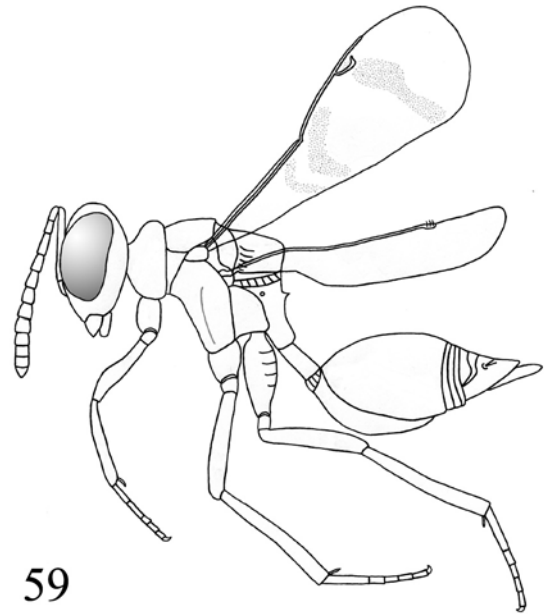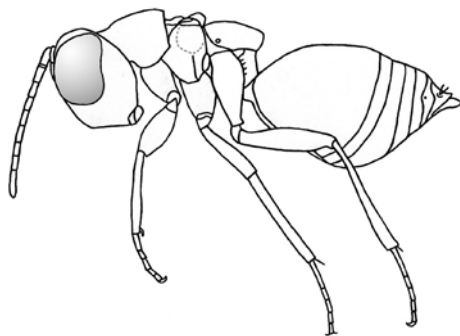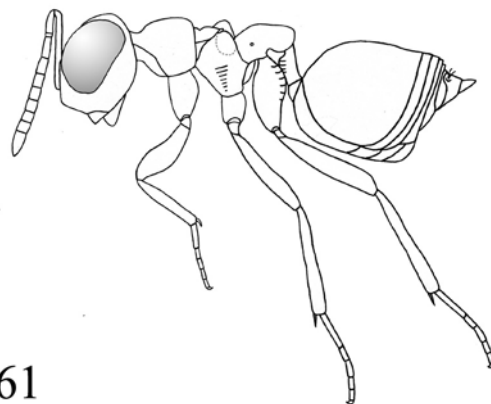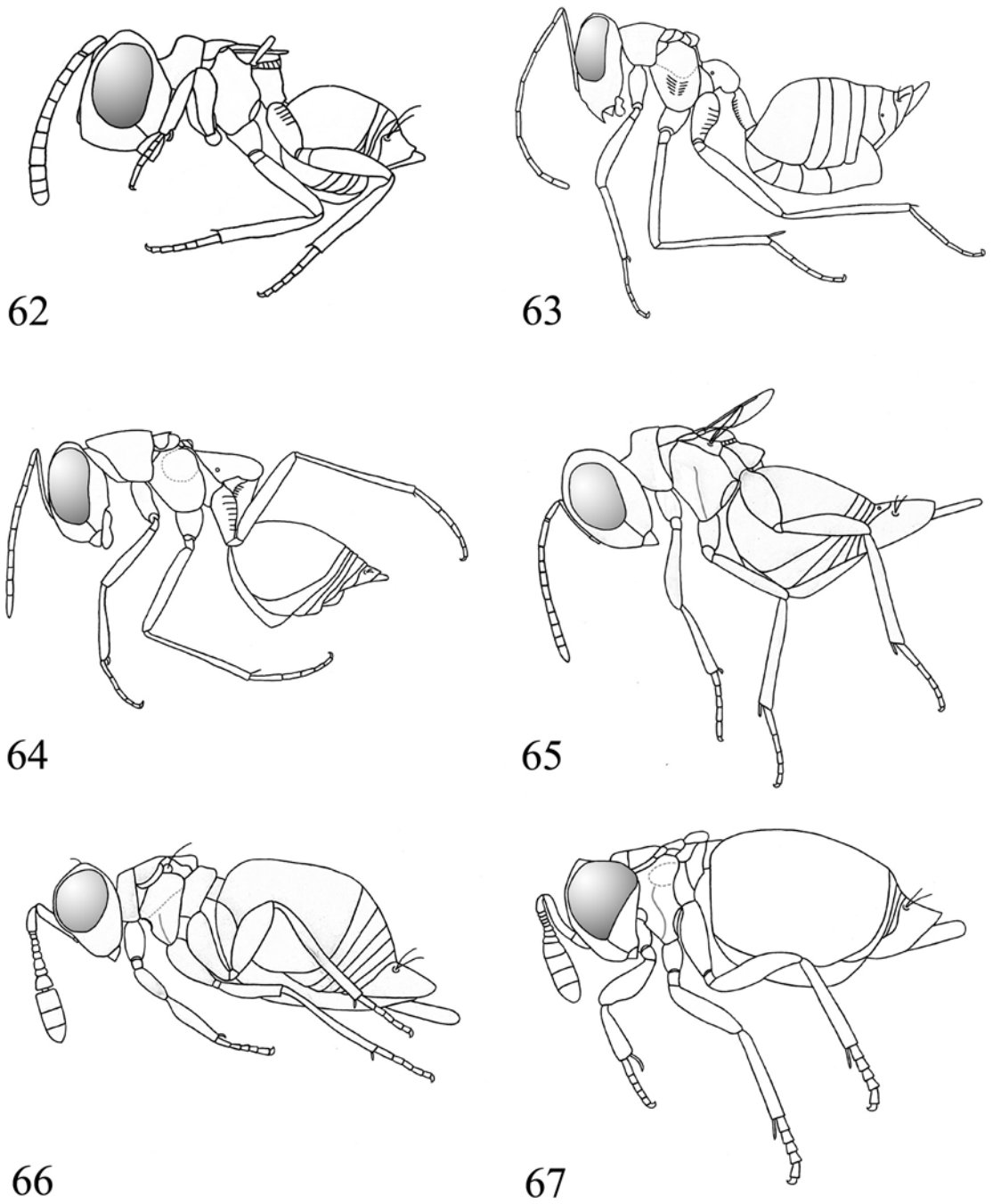
Figures 56-61. Lateral habitus views: 56, *Neapterolelaps viridescens*; 57, *N. mitteri*; 58, *Cerodipara sabensis*; 59, *Chimaerolelaps villosa*; 60, *Conophorisca littoriticus*; 61, *C. n. grisselli*.

Figures 62-67. Lateral habitus views: 62, *Dozodipara insularis*; 63, *Myrmicolelaps iridius* 64, *M. aurantius*; 65, *Lelaps noorti*; 66, *Nosodipara ferrana*; 67, *Pseudoceraphron regieri*.
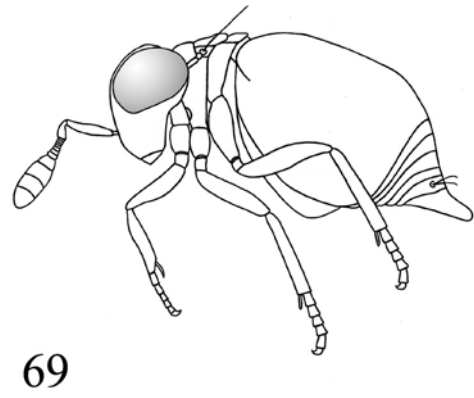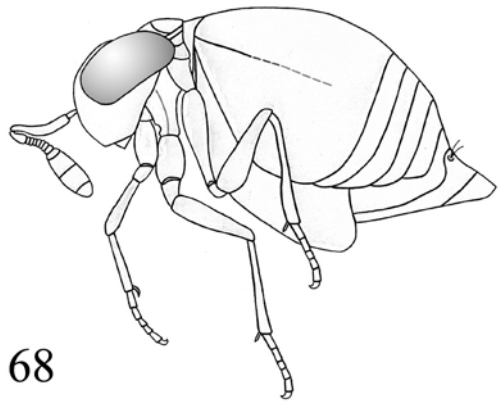
Figures 68-69. Lateral habitus views: 68, *Pseudoceraphron fijensis*; 69, *P. burwelli*.

Figure 70. Maximum likelihood tree based on a GTR+Γ+I model including all nucleotides. Bootstrap percentages >50 are shown above the corresponding branches. Higher classification is listed to the right of the taxa. Names ending in –dae represent family names of non-pteromalid taxa. Names ending in –nae represent non-pteromalid subfamily names.

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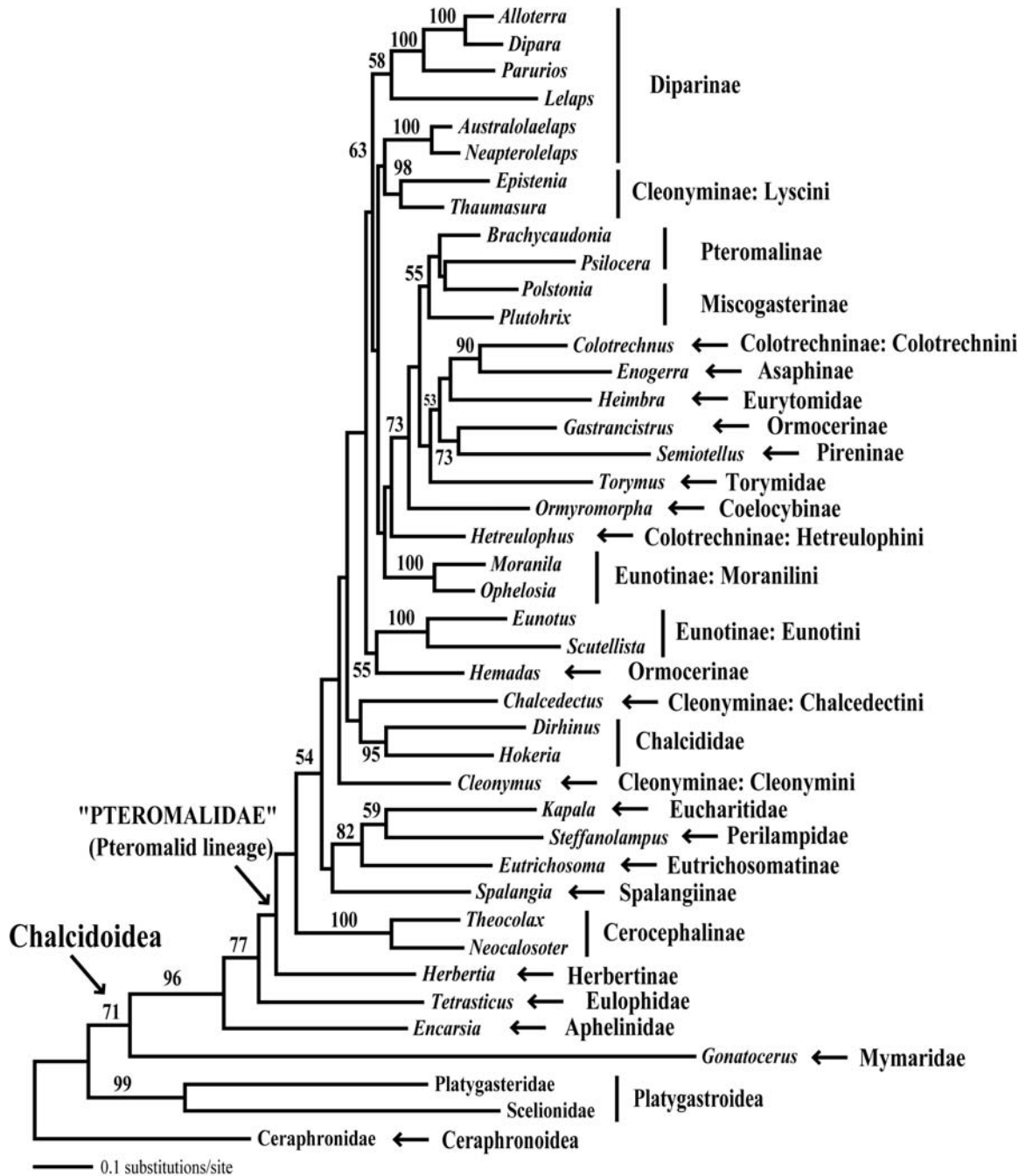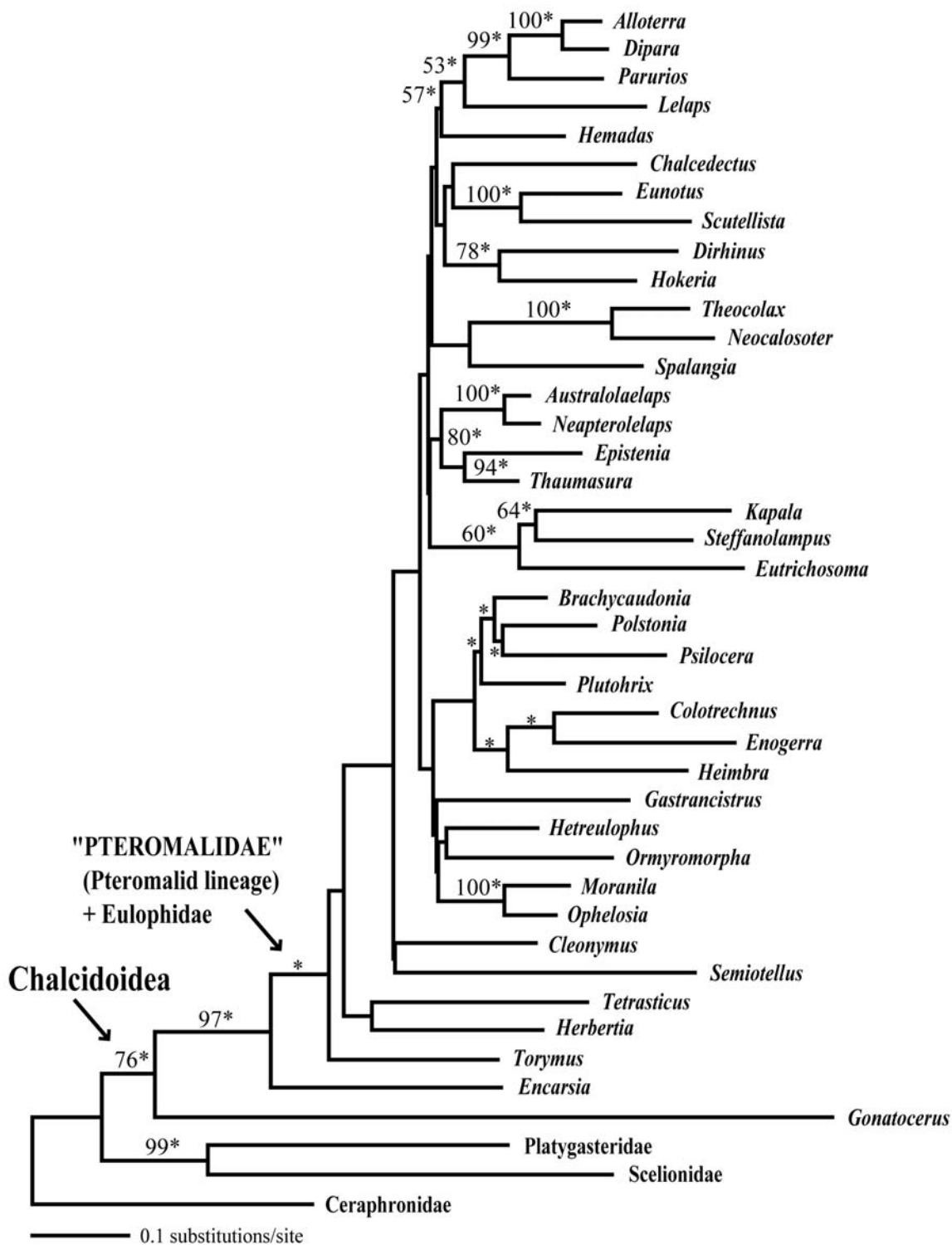**Figure 71.** Maximum likelihood tree based on a GTR+Γ+I model excluding nt3. Bootstrap percentages >50 are shown above the corresponding branches. Branches marked with an "*" were also recovered in the all-nts analysis.

APPENDIX I

Character coding for morphological phylogenetic analysis. Numbers in "()" denote

polymorphism. Numbers in "{}" denote ambiguity. Names in "()" refer to the

classification of the taxon prior to this study. Names followed by "*" refer to units in the

phylogenetic analysis, and do not represent valid names.

Lelaps noorti   100001001000000001000????????030110000010100000100000

00000??000?010111????00

Cerodipara sabensis   200000000010100000001000?00100301100023101100000000100

00100??000?010111????01

Boeria   300000000001100000001110?111013011000200010000000100

00100??000?0101111???01

Spalangiopelta   00110000000010200000(01)(02)(01)(02)?(03)(01)(02)004000003

000000000010000000001100000001101(01)1111

Calolelaps   110{12}00001000101000000????????0400000000000000001000

10000000110100000000???00

Mesolelaps   100000001000100000000????????0400000000100000001000?00

00000100000100000???00

Neolelaps   100100000000101010000????????0400000000000000001000100

00000100000000000???00

Stictolelaps   100{12}000010001010(12)0000????????04000000000000000010

00100000001001000000000???00

Ormyromorpha   0001000010101120202010 00?0110011??000000000000001000000

1000000000000001000??100

Lelapsomorpha   200100000010112020201201?3210011??000000000?0001000000

(01)000000000000 1000??100

Eunotus   010210001(01)01(01)(01)0120000????????0400000000010001000

100000001000000001100000??000

Moranila   010210001(01)00110120001012?2110040000000 0102000001000

0000000000 0001110000??000

Neapterolelaps (Australolaelaps)   01011100000100001 0000????????0400000000101

0000010000001101100000 11111111000

Neapterolelaps   011111000001100000000????????0202?0011210100 0001000000

1110110011011111112000

Neapterolelaps viridescens   0101110000011000200 00????????0400000000101000001

0000001110??000 10111111??000

Neapterolelaps mitteri   010111000001100020000? ???????0400000000101000001

0000001110??000101 11111??000

Liepara   2002000000001000200120111110040000000000000000 00100000

00100000000 0101100??000

Pseudoceraphron (Dipareta) albifrons   010{12}0000010020402?011000?1000020

2?00433111301100110001000 1??000?1101111???00

Pseudoceraphron (Malinka) nana   01020000110020402?011000?10110202?1

04311113011001100010001??000?1101111???00

Pseudoceraphron pulex   01021000110020402?010????????0400000431111301100 1100010001??000?1101111???00

Pseudoceraphron (Dipareta) regieri   010{12}1000010020402?010????????0202 ?00413111301100111001?001??000?1101111???00

Pseudoceraphron burwelli   01021000110020402?011000?101004000043111130110 01100010001??000?1101111???00

Pseudoceraphron (Malinka) fijensis   01021000110020402?011000?00110202?10 4311113011001100010001??000?1101111???00

Nosodipara monteithorum   00111000000203020010????????1202?0022311100010011 110010000??000?0101111???00

Nosodipara ferrana   00011000000203021011100?00001202?0021311100010011100 10000??000?0101111???00

Pondia   3003100000001000200011120?11002202?00321001200000000000 0100??1020010111122000

Pyramidophoriella   300{12}0000000010000000????????002???022011120000010?? 000100??000?000111????00

Conodipara scutellata   20000100100100001010100????????2301100213111200000 0011010100??12000101110??000

Conophorisca anullata   20000101000?0000?0?00????????2301100221111200020 001?010100??11000101110??000

Myrmicolelaps (Dolichodipara) scutellata   20000100000100001020 0????????2301101 22112120002000111101 00??11000101110??000

Conophorisca littoriticus   20000101000000000000100????????2301100221111200020

0011010100??11000101110??000

Conophorisca grisselli   30000101100000000200????????2301100221111200020

0011010100??11000101110??000

Myrmicolelaps (Dolichodipara) iridius   20000100?0010000102 00????????2301101

221121200 0200011110100??11000101110??000

Myrmicolelaps paradoxus   20001000100100001 0200????????3601000521111000020

0011110100??11000101110??000

Myrmicolelaps aurantius   200000000001 0000{01}0200????????1701301521111400

0200011110100??11000101110??000

Dipara (Grahamisia) 300??10000001000{01}0001101011001202?10000001000001000

10001001100100 10111122000

*Dipara sensu stricto**   3000(01)10000001000{01}00011(01)10111013011000000

01(04)0000100010001001100100 10111122000

Dipara (Australian Dipara*) 301{01}?100000(01)10(01)0200011111111100(46)0(01)00

00000010100010000000100110010010111122000

Dipara (Parurios)   3000?10000001000000011110111005012000000010200 01000000

0100110010010111100000

Dipara turneri   3011111000001000{01}0001100?1100050120000000 1000001000

0000100??001?0101111???00

Dipara (Fiji Dip/Par*)   300{01}111000001000{01}0001120?11000511200420111

40000100 00000100??001?0101111???00

Dipara (Indonesian Pondia*) 300{12}?1000000100000001101011002501200300001000

001000(01)000100??00100 10111122000

Dipara (Micro Dipara*)   300{01}?0000000100020011010111006010(01)0000001

000001000000010011001?0101111???00

Netomocera   3000?10000001100(012)(01)001111?111004000000000001000001

000(01)0001001100000101111110000

Lelaps   100001000000100011001111?11100(46)0(01)0000000010(01)000

1000(01)0001001100(01)0010111111000

Lelaps (Spalangiolelaps)   100001000000100011001111?11100301100000101000001

000100010011000010111111000

Dipara (Alloterra)   300{01}00001000102020000????????1601000311101400001000

10101001100100101111100000

Dipara (Pseudipara) 200200000001101020001101011100601000000101000001000000

0100111010010111122000

Cea   000{01}01001000002000000????????0400000000000000001000

10000001100000001000??111

Bohpa   00010100000002020000????????0400000643111100000000000

0000??000?0001101???01

Dozodipara   200{01}0101000010000000????????03011007001011?0000000

(01)010100??000?010111????00

Chimaerolelaps   3000010000001000{01}?001301112100400000000001010001000

(01)000100110100101111111000

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