A MORPHOLOGICAL EVALUATION OF THE SUB-APICAL DORSAL NOTCH IN THE FAMILY ICHNEUMONIDAE (HYMENOPTERA) AND ITS APPLICATION TO A REVISION OF THE GENUS *Hodostates* FOERSTER

A Thesis

by

MIKA D. CAMERON

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2009

Major Subject: Entomology

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Approved by:

Chair of Committee,	Robert A. Wharton
Committee Members,	Thomas Stidham
	James B. Woolley
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ABSTRACT

A Morphological Evaluation of the Sub-apical Dorsal Notch in the Family
Ichneumonidae (Hymenoptera) and Its Application to a Revision of the Genus
Hodostates Foerster. (August 2009)

Mika D. Cameron, B.S., Texas A&M University, College Station
Chair of Advisory Committee: Dr. Robert Wharton

A detailed study of ovipositor morphology in Ctenopelmatinae (Ichneumonidae) is provided and used to assess the evolutionary patterns of the Ophioniformes, Ctenopelmatinae, and more specifically the tribe Pionini (Ctenoplmatinae). Ovipositor morphology also provided a foundation for a generic revision of *Hodostates* Foerster, 1869.

Monophyly of Ophioniformes, as defined by Gauld and Wahl, is not supported by research provided in this thesis. Morphological characters previously used to unite Ophioniformes are also found in non-ophioniform subfamilies, leaving the ophioniformes without a morphological synapomorphy.

Research on the tribe Pionini, as currently defined by Townes, led to the hypothesis that pionines are polyphyletic with likely evolutionary affinities including, but not limited to, Mesoleiini and Perilissini.

The genus *Hodostates* Foerster, 1869 has been revised. Work presented in this thesis is the first comprehensive comparison of both Nearctic and European species. This study resulted in the transfer of *Hodostates schaffneri* Hinz, 1996b to *Lethades* Davis.

DEDICATION

To my husband, John.

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I would like to thank, first and foremost, Dr. Robert Wharton for affording a budding morphologist the opportunity to pursue a research project that was as rewarding as it was challenging. I also greatly appreciate his eagerness to provide direction and assistance throughout the entire duration of this project. As chair of my committee, he always allowed me to participate in activities and courses that would better prepare me as an educator. Dr. Wharton's excitement of research and teaching was contagious, and frequent conversations of topics outside the realm of entomology led me to think beyond the parameters of ichneumonid ovipositors. I also would like to thank additional committee members, Drs. James Woolley and Thomas Stidham, for their ongoing guidance and support, as well as the following curators or collection managers and institutions for providing loan material: David Wahl (AEI), Jason Weintraub (ANSP), Gavin Broad (BMNH), Jens-Peter Kopelke (NHMS), Robert Kula (USNM), Roy Danielsson (MZLU), and Stefan Schmidt (ZSM). I give special thanks to Heather Cummins and Patricia Mullins for braving the cold temperatures of the collections room for hours at a time in order to take the great pictures presented in this thesis. Of special recognition was the patience and understanding exhibited by my husband, John, who allowed me to pursue a graduate degree.

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CHAPTER I

INTRODUCTION

Parasitism

Seven hexapod orders have a parasitoid lifestyle. Amazingly, 80% of parasitoid species are hymenopterans (Quicke 1997). A parasitoid is an organism that develops on or in another ("host") organism, extracts nourishment from it, and kills it as a direct or indirect result of that development, typically laying their eggs on or in the host's immature stages (Eggleton and Gaston 1990, Belshaw *et al.* 2003). Parasitoids differ from parasites based on the parasite's need of a living host, with death of the host generally considered to be non-adaptive for a parasite. The most widely accepted hypothesis suggests that the parasitoid lifestyle in Hymenoptera arose once in the common ancestor of Orussoidea + Apocrita (Gibson 1985). This hypothesis entails an origin from a foundation based on specializations for larval feeding within tunnels in wood and at least partly upon fungi (Eggleton and Belshaw 1992, Quicke 1997, Whitfield 1998, Wharton *et al.* 2004).

One of the most conspicuous features of an insect parasitoid is whether its larvae

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develop externally or internally (Quicke 1997). External larval development is denoted as ectoparasitic; whereas internal larval development is referred to as endoparasitic. In addition to the external/internal dichotomy, the hosts of some parasitoids continue their development for a varying period of time following oviposition (koinobiosis), while others are permanently paralyzed, with no further development (idiobiosis). One of the most striking features of life history evolution among parasitoids is the transition from idiobiosis to koinobiosis (Askew and Shaw 1986; Belshaw and Quicke 2002). Idiobionts often are characterized by morphological adaptations associated with gaining access to hosts, whereas in koinobionts, physiological adaptations are necessary to combat a host's defense (Quicke 1997).

Idiobiosis

Although exceptions occur, most idiobionts are ectoparasitoids. Idiobiont ectoparasitism of concealed hosts generally is considered to be the basal form of the parasitoid lifestyle (Wharton *et al.* 2004). Overall, an idiobiont has a broader range of hosts than a koinobiont. In part, this is, because most idiobionts permanently paralyze their hosts prior to oviposition, and thus the developing larvae do not have to adapt to host-specific immune systems. Gauld (1997) refers to a parasitoid's "searching niche", and states that an idiobiont will attack any host present in their niche, therefore being more specific to a niche rather than its hosts. However, this lack of host specialization is correlated with vulnerable egg placement. Vulnerability of an exposed, immobile host (to other natural enemies, as well as environmental factors) means that female idiobiont parasitoids may be largely constrained or limited to attacking a concealed host, where the developing larvae will be more protected (Gauld 1988). Attacking concealed hosts (most commonly in plant tissues and galls) requires morphological adaptations, such as an ovipositor than can function in part as a drill, to locate and gain necessary access to the host (Gauld 1988).

Idiobiont endoparasitism is relatively rare, and generally confined to cases of egg and pupal parasitism, where the host is immobilized or rapidly killed to prevent development to the next stage. Gauld (1988:358) states that an idiobiont endoparasitoid "is merely feeding on the incapacitated host from the inside rather the outside." Most commonly, idiobiont endoparasitoids attack lepidopteran hosts in cocoons (Gauld 1988).

Koinobiosis

Among the Ichneumonidae, the family of interest in this investigation, endoparasitic koinobiosis is by far the dominant lifestyle (Gauld 1988). The eggs of koinobiont parasitoids are deposited variously inside the host's body, including attachment to the gut wall, placement inside internal organs such as fat bodies and ganglia, or released into the haemocoel (Gauld 1984). Once inside the host, koinobionts must integrate with host physiology and combat defense mechanisms of the host such as encapsulation (Vinson and Iwantsch 1980). Due to such "environmental pressures" (Gauld 1984), one can assume a more narrow host range, when compared to an ectoparasitoid or idiobiont, because of the close parasitoid-host relationship.

Some koinobionts are ectoparasitic, and this lifestyle is perhaps best known in the Ichneumonidae. According to Gauld (1991), ectoparasitic koinobiosis has evolved separately in the following three subfamilies: Tryphoninae, Adelognathinae, and the polysphinctine Pimplinae (that attack arachnids). The primitive form of ectoparasitic koinobiosis is presumed to be present in adelognathines, in which Fitton *et al.* (1982) observed both idiobiont and koinobiont lifestyles. Characterization of adelognathines as "primitive" is based on their parasitoid eggs being glued to the host, and the location of parasitoid pupation (Gauld 1991). It is thought by Gauld (1991) and Fitton *et al.* (1982) that their behavior of rapid egg hatching and larval growth is due to the inability to avoid being discarded during the host larva's penultimate ecdysis, a true obstacle to ectoparasitism. However, specialization arose in the tryphonines in which a stalked egg serves functionally as an anchor to the host (Gauld 1991).

As Gauld (1991) mentions, this specialization allows egg retention on the host during its penultimate ecdysis, after which the host forms a cocoon, the parasitoid egg hatches, and the parasitoid larva feeds on the host in a concealed environment. Gauld (1991) and Kasparayan (1981) specify that tryphonines have adopted ways to prevent egg desiccation by attacking hosts in humid environments, and additionally that careful placement of eggs prevents predation by the host. The change from ectoparasitism to endoparasitism is another way to solve problems such as desiccation and vulnerability (Gauld 1991). Gauld (1991), for example, illustrates how internal egg placement prevents dislodging during any host stage.

The transition between such biologically different lifestyles (ectoparasitism and endoparasitism) should be accompanied by morphological changes, including, perhaps, those associated with the ovipositor. Detailed exploration of character systems from a functional morphological standpoint also should improve classifications. It is with this in mind that I have examined ovipositor morphology of the family Ichneumonidae, the largest family of Hymenoptera in terms of number of described species, approximately 21,000 (Yu and Horstmann 1997). A long association between koinobiont ectoparasitoids in the subfamily Tryphoninae and koinobiont endoparasitoids in the subfamily Ctenopelmatinae provide a good starting point for such a comparison. Prior to Townes (1969), tryphonines and ctenopelmatines usually were placed within the same subfamily. More recently, Gauld (1997) noted that males of these two taxa are difficult to assign properly to subfamily.

Ichneumonid Classifications

Townes (1969) recognized 25 subfamilies of Ichneumonidae, and this number has steadily increased to about 40 (Gauld *et al.* 2002; Quicke *et al*., 2005). Using the arrangement of subfamilies in the Townes volumes, Gauld (1985), Wahl (1991, 1993a) and Wahl and Gauld (1998) established informal groupings of subfamilies, basing these on discrete characters hypothesized as synapomorphies. These informal groupings have been recognized and used by all subsequent workers, and most notably by Belshaw and Quicke (2002) and Quicke *et al*. (2005). The three largest of these groupings are the basal Pimpliformes, the Ichneumoniformes, and the Ophioniformes (Table 1).

Wahl (1990) erected a monophyletic informal grouping, the Pimpliformes, comprising eight subfamilies: Pimplinae, Rhyssinae, Diacritinae, Poemeniinae, Acaenitinae, Cylloceriinae, Orthocentrinae and Diplazontinae. Wahl and Gauld (1998) defined Pimpliformes on the basis of larval and adult characters, with basal members having stout ovipositors. They hypothesized that ancestral Pimpliformes were idiobiont ectoparasitoids of holometabolous insects concealed deeply in plant tissue.

Wahl (1993b) proposed the informal name of “Ichneumoniformes” as a monophyletic grouping of three subfamilies: Ichneumoninae, Brachycyrtinae, and Cryptinae. Based on the ectoparasitic nature of the Brachycyrtinae, Wahl (1993b) proposed that the common ancestor of the Ichneumoniformes was most likely an ectoparasitoid that oviposited into silk. There is variation between the ovipositors of ichneumonines and cryptines. Cryptines have long ovipositors, often attacking concealed hosts, and ichneumonines have short ovipositors attacking larvae and pupae that are sometimes weakly concealed in leaf litter (Townes 1970b).

Ophioniformes is a monophyletic group proposed by Gauld (1985) and it is supported by three synapomorphies: possession of a dorsal sub-apical notch on the ovipositor, possession of similar female reproductive tract, and having endoparasitic larvae that lack a labral sclerite and possess a Y-shaped prelabial sclerite. Based on the distribution of these character states, Gauld (1985) included the following subfamilies in Ophioniformes: Ophioninae, Campopleginae, Cremastinae, Tersilochinae, Banchinae, and Ctenopelmatinae. Wahl (1991, 1993a) later redefined Ophioniformes by adding

Tatogastrinae and Anomaloninae, and also discredited the reproductive tract and prelabial sclerite synapomorphies. Belshaw and Quicke (2002) and Quicke *et al.* (2005) later included Mesochorinae, Metopiinae, Lycorinae, Neorhacodinae, Oxytorinae, Phrudinae, Stilbopinae, and Tryphoninae.

Pampel (1913) found that Banchinae, Ctenopelmatinae, and Ophioninae (s.l.) have similar female reproductive tract morphologies: large number of ovarioles (15-40) per ovary, and lateral oviducts at least 1-2x as long as the ovaries and filled with mature eggs. This *Ophion*-type reproductive tract appears to be an apomorphic condition, while the plesiomorphic condition is represented in Pimplinae, Xoridinae, and Cryptinae (Wahl 1991). Wahl (1993a) excluded the derived form of the ovaries as a synapomorphy of Ophioniformes because mesochorines and metopiines both possess the *Ophion*-type reproductive tract. Wahl may have excluded this character based on the original set of subfamilies included in Ophioniformes, but the broader set of subfamilies included by Belshaw and Quicke (2002) may leave this synapomorphy intact. Belshaw and Quicke (2002) did not discuss specific characters supporting the inclusion of these additional taxa in Ophioniformes, so the validity of this synapomorphy remains to be examined.

According to Wahl (1991), the only subfamilies to possess the Y-shaped prelabial sclerite are Campopleginae and certain Banchini. Other banchines and isolated ctenopelmatines possess a band-shaped prelabial sclerite, while a triangular prelabial sclerite is found in cremastines and ophionines (Wahl 1991). The cremastine form (triangular) is thought to be the precursor for the Y-shape in Campopleginae, suggesting that Campopleginae and Cremastinae are sister groups (Wahl 1991). However, Banchini demonstrate the development of a Y-shaped prelabial sclerite from the bandshaped prelabial sclerite, therefore, either form can be a precursor (Wahl 1991).

The ovipositor notch is the only synapomorphy for Ophioniformes left intact by Wahl (1991,1993a). A well defined notch is present in all subfamilies originally included in Ophioniformes by Gauld (1985), most notably Ophioninae, Campopleginae, Cremastinae, Ctenopelmatinae, Banchinae, and Tersilochinae (although poorly developed in many tersilochines). However, this character is not present in most of the taxa included in Ophioniformes by Belshaw and Quicke (2002). This study examines morphological variation of the ovipositor in one of the originally included members of the Ophioniformes, the Ctenopelmatinae.

Ctenopelmatinae

Classification

Ctenopelmatinae (= Scolobatinae *sensu* Townes 1970b) is a large, mainly North Temperate, subfamily with worldwide distribution of approximately 100 genera and 1,200 species (Townes 1970b; Gauld 1984; Gauld 1997; Yu and Horstmann 1997). Originally, Townes (1970b) recognized eight tribes: Westwoodiini, Ctenopelmatini, Olethrodotini, Pionini, Perilissini, Scolobatini, Mesoleiini, and Euryproctini. Gauld (1984) later combined the Westwoodiini with the Scolobatini on the basis of four shared, derived features. Although Townes (1970b) and Gauld (1984) treat Scolobatini, Olethrodotini, and Ctenopelmatini as being quite distinctive, the tribes Perilissini, Mesoleiini, and Euryproctini are very large, poorly delimited, and contain many very poorly defined genera. This lead Gauld (1997) to conclude that the classification of the Ctenopelmatinae is probably the least satisfactory of any ichneumonid subfamily.

Prior to the work of Townes (1945, 1951, 1969, 1970), members of the Ctenopelmatinae where primarily included in the Tryphoninae. Tryphonines and ctenopelmatines, more specifically males, are often difficult to identify to subfamily. Gauld (1997) provides a list of the most useful morphological characters for distinguishing ctenopelmatines from tryphonines, including: small tooth on outer distal margin of fore tibia, sub-apical dorsal notch on ovipositor, fore wing *2m-cu* with one or very rarely two bullae, first flagellomere sometimes with tyloid on outer side, apical fringe on clypeus lacking, mandibles not or weakly tapered, with the lower tooth from smaller to larger than the upper, and mesoscutum without small projection laterally behind tegula. Unfortunately, there are exceptions to nearly all of these features. Thus, in addition to adult morphology, Gauld (1997) observed that biological differences and associated differences in larval morphology have contributed to the continued recognition of two separate subfamilies. Gauld (1987) also acknowledges ctenopelmatines as one of the least specialized koinobiont ichneumonids.

Biology

Ctenopelmatines are koinobiont endoparasitoids of exposed, leaf feeding larval symphytans, and, more rarely, of lepidopterans (Gauld 1987, 1997). Although the majority of the rearings are from tenthredinoid and megalodontoid sawflies (Townes

1970b), Barron (1994) and Gauld (1984) provide specific examples of the few ctenopelmatines that attack lepidopteran hosts. The northern distribution of ctenopelmatines is correlated with tenthredinoids having highest diversity outside the tropics (Gauld 1987). The host stage attacked is variable among tribes ranging from eggs to all larval stages (Graham 1953, Townes 1970b, Pschorn-Walcher and Zinnert 1971).

Ctenopelmatine egg size varies considerably interspecifically. Pionines have the smallest known eggs, subspherical and 0.10 mm in diameter, while in other tribes the eggs may be over 0.80 mm long and sausage-shaped (Gauld 1997). According to Bronskill (1960) and Griffiths (1975), oviposition generally occurs in the haemocoel of the host through the softer sterna, however Eichorn (1988) noted that some species of *Homaspis* are known to oviposit into the nerve ganglia or into other internal organs. Pionines often have been assumed to oviposit in host eggs, and that explains the small size of their own eggs.

As with other ctenopelmatines, pionines are endoparasitoids of sawflies. The host stages attacked include very young larvae and eggs (Townes 1970b). Pionine eggs are the smallest of the Ctenopelmatinae. Eggs of *Rhorus lapponicus* Roman are 0.18 mm in length and those of *R. exstirpatorius* 0.10 mm in length; both are round-oval in shape. Eggs of *Trematopygus sp.* are about 0.30 mm in length and kidney shaped (Pschorn-Walcher and Zinnert 1971). The genus *Rhorus* is an exception to the egg parasitoid lifestyle. Pschorn-Walcher and Zinnert (1971) give a biological overview of this unique group of parasitoids. The species of *Rhorus* that they studied attack first and second larval instars of its main host, *Pristiphora wesmaeli* Tischbein (Hymenoptera: Tenthredinidae), a pest of larch. According to Pschorn-Walcher and Zinnert (1971), oviposition is always through the ocellus of the host's head capsule lasting approximately 20-30 seconds. The parasitoid hatches after the host has spun its cocoon. The small eggs of pionines, regardless of where they are placed, are associated with a needle-like ovipositor that lacks the notch characterizing the subfamily as a whole.

Ovipositor Morphology

The evolution and specialization of the parasitoid lifestyle are presumably forces that drive morphological and anatomical changes to the ovipositor. The extreme diversity represented in Ichneumonidae leads to an array of utilization strategies reflected by morphological adaptations that are apparent at most taxonomic levels. Townes (1970b), in establishing his classification of the Ichneumonidae, used morphological characters associated with the ovipositor as diagnostic features at all taxonomic levels.

Basic Morphology

Although morphological structures may differ, a generalized form exists. Snodgrass (1935) and Scudder (1971) define the ovipositor as originating from the gonapophyses of the eighth and ninth abdominal segments, that collectively function for deposition of eggs. In simplified terms, Quicke *et al.* (1999) state that the upper and lower valves form the ovipositor proper.

The upper valve, commonly referred to as the second valvifer, is the product of fusion between the two gonapophyses of the ninth abdominal segment. Quicke *et al.* (1994) state that basally, the two gonapophyses retain separate lumens, and are connected ventrally and dorsally by layers of membranous cuticle. More apically, the two gonapophyses are completely fused. Symphytans are an exception because they tend to have the upper valves completely divided basally, though this is not true of orussids. In at least some members of the Ichneumonidae, the upper valves of the ovipositor have a mid-dorsal groove basally. All apocritans have the upper valve undivided at the apex (Quicke *et al.* 1994).

The lower valves are gonapophyses of the eighth abdominal segment and are commonly referred to as the first valvifer and are never fused. The conjunction of the upper and lower valves produces the egg canal. The mechanism through which the upper valve and lower valves interlock and slide along each other is referred to as the olistheter (Smith 1969). The olistheter is a tongue and groove mechanism comprised of the “T” section, the rhachis (located ventrally on the upper valve and the complementary groove), the aulax, located dorsally on each lower valve (Rahman *et al.* 1998; Quicke *et al.* 1994; Quicke *et al.* 1999). Quicke *et al.* (1994) also note inconsistency in the olistheter’s point of termination. In pictoral detail, Rahman *et al.* (1998) show similarities of rhachis termination points along the ovipositor between braconids and ichneumonids that share similar biologies, and use this information to determine a plesiomorphic condition or groundplan state. For example, a species of poemeniine ichneumonid and cyclostome members of the family Braconidae possess a rhachis that terminates well before the apex of the ovipositor. All of these species are ectoparasitoids. Similarly, endoparasitic banchines and endoparasitic braconids both possess a rhachis that reaches the apex of the ovipositor. Rahman *et al.* (1998) propose that since the ancestral biology of ichneumonoids is idiobiont ectoparasitism, a rhachis that does not reach the apex of the ovipositor is therefore plesiomorphic.

Articulated, chitinous flaps known as valvilli (singular = valvillus) are sometimes present protruding into the egg canal from the lower valves or sometimes from both upper and lower valves. The presence of at least one valvillus is a synapomorphy for the sister-grouping of Ichneumonoidea + Aculeata (Quicke *et al.* 1992). The number of valvilli varies from zero to seven (the latter found in some species of *Pion*) (Quicke *et al.* 1992), and position differs greatly from basally to near the apex of the ovipositor. Quicke *et al.* (1992) propose the function of valvilli is to retain the egg in proper position until the exact moment needed for oviposition.

The posterior parts of the ninth gonocoxite form a pair of ovipositor sheaths that enclose and protect the ovipositor proper at rest (Quicke *et al.* 1999). Quicke *et al.* (1999) give probable functions of these sheaths as protection, for cleaning of the ovipositor proper, and for bearing sensory structures used when searching for concealed hosts.

The Ovipositor Tip

Ovipositors in ichneumonoid wasps vary greatly in length from short and largely hidden by the subgenital plate to being extruded one or more times the length of the body. In very short ovipositors, the entire length may contain features of interest in understanding the wasp's biology, but in long ovipositors, the tip of an ovipositor serves as a window into an organism's biology. Differences between ectoparasitism and endoparasitism are reflected in the morphology of the ovipositor. Serrations or teeth are located on the ovipositor tip. Serrations are the modified remnants of the multisegmented lamnium of the upper and lower valves (Quicke *et al.* 1994). Placement of serrations are used in Hymenoptera classification at many taxonomic levels; for example, symphytans possess serrations on the upper and lower valves, chalcidoids and megalyroids house serrations on the upper valves and ichneumonoids bear serrations on the lower valves (Quicke *et al.* 1994). Quicke *et al.* (1999) list the following two functions of serrations: tearing the substrate and providing support during drilling. Serrations on ovipositors are thus predicted to be more conspicuous on parasitoids of concealed hosts rather than exposed hosts (Quicke *et al.* 1999). As mentioned in Quicke *et al.* (1994), frequently near the apex a notch, or a nodus protrudes on the valve opposite the valves equipped with serrations. The nodus is present in ectoparasitoid ichneumonid subfamilies such as Cryptinae, Xoridinae and Pimplinae (Rahman *et al.* 1998).

Species with a nodus lack a sub-apical notch, and vice versa. There is a strong correlation between possession of a notch and koinobiont endoparasitism attacking larval instars. Nearly all members of the Ophioniformes senu Gauld (1985) and Wahl (1991, 1993) have a sub-apical dorsal notch and are koinobiont endoparasitoids of holometabolous insect larvae. Functionally speaking, the sub-apical notch in ichneumonids may be analogous to the "ovipositor clip" discovered by van Lenteren *et al*. (1998). The ovipositor clip mechanism was described by van Lenteren during his studies of the eucoilid cynipoid, *Leptopilina heterotoma* (Thompson), that attacks larvae of *Drosophila*. The wasp possesses a “deep, denticulate transverse groove” located on the morphological upper valve sub-apically. Function of the clip is to grip the torn cuticle of the host directly after the parasitoid’s initial penetration in order to prevent the host trying to escape through physical means such as rolling or crawling (van Lenteren *et al*. 1998). Whether the notch in eucoilines functions in exactly the same way as the notch in ichneumonids is doubtful since some elements seem to be missing, but there is the possibility of an analogous function.

The presence of this notch located sub-apically on the ovipositor is of interest due to its role in establishing monophyly of the informal ichneumonid grouping Ophioniformes: the possession of this sub-apical dorsal notch is one of three putative synapomorphies originally proposed by Gauld (1985). The other two synapomorphies were dismissed later by Wahl (1991, 1993a), but the ovipositor notch has essentially been ignored. Quicke *et al.* (2005), for example, do not include the ovipositor notch in their morphological analysis although they do include Gauld’s (1985) labral sclerite feature. Ctenopelmatinae are one of the originally included members of the Ophioniformes, but not all ctenopematines have a notched ovipositor (Townes 1969, 1970b), as noted in the above discussion of pionines. The question then arises as to whether there are any ovipositor features that can be used to support the monophyly of either the Ophioniformes or the Ctenopelmatinae.

Research Objectives

The primary objective of this thesis is a comparative morphological study of the ctenopelmatine ovipositor, with a focus on the sub-apical notch. The specific objectives are to (1) develop a set of unambiguous characters and character states useful for describing variation in ctenopelmatine ovipositors; (2) use this dataset to determine whether Ophioniformes, Ctenopelmatinae, and the major ctenopelmatine tribes can be characterized as monophyletic on the basis of the ovipositor; and (2) use data on ovipositor morphology to revise *Hodostates* Foerster and assess its placement within the Ctenopelmatinae.

CHAPTER II

CHARACTERIZING CTENOPELMATINE OVIPOSITORS

Introduction

Townes (1969, 1970b) used several ovipositor characteristics to support his proposed reclassification of the family Ichneumonidae. For example, Townes (1970b) described the ctenopelmatine ovipositor as usually not longer than the apical depth of the metasoma, with Olethrodotini being the exception. The ctenopelmatine ovipositor also possesses a sub-apical dorsal notch (unless the ovipositor is very slender) and the serrations on the lower valves are lost or reduced. However, loss of serrations on the lower valves is common in koinobiont endoparasitoids (Quicke *et al.* 1999), and thus it is characteristic of several other subfamilies besides Ctenopelmatinae.

Some of the variation in ovipositor morphology is reflected in tribal classification of the Ctenopelmatinae, but some is not. For example, Quicke *et al.* (1994) noted that in the upper valve, the presence of a septate lumen and the extent of the notal membrane do not correlate with current tribal classifications of Ctenopelmatinae. The division of the upper valves by a notal membrane was proposed by Quicke *et al.* (1994) to facilitate distortion of the upper valves in conjunction with the lower valves to increase surface area for passage of the eggs. Distortion of the dorsal valves is beneficial to ctenopelmatines where the eggs are dark and relatively hard (Quicke *et al.* 1999). Similarly, Townes

(1970b) describes the perilissine form of the notch as varying from strong (Figs. 1-4) to shallow (Figs. 5-10) or even sometimes absent as seen in Fig. 11. On the other hand, mesoleiine ovipositors, with the exception of *Anoncus* (Townes 1970b) (Fig. 12), are deeply notched and thick at the base.

A needle-like ovipositor is diagnostic for the tribe Pionini (Townes 1970b). Brajkovic *et al.* (1999) conclude that with the development of egg-larval parasitism, the upper and lower valves converge on a needle-like form in several different taxa. The pionine ovipositor fits this characterization as it is thick at the base (concealed by the hypopygium) and terminates into a very slender, needle-like ovipositor (Fig. 13-16). Townes (1970b) concludes that the lack of the sub-apical notch is a diagnostic feature of the Pionini, but notes that two of the genera, *Labrossyta* Foerster (Fig. 17) and *Hodostates* Foerster (Fig. 18) possess a weak notch. Townes (1970b) goes on suggest that these two genera do not belong in Pionini, though he failed to place them elsewhere.

The degree of variation already noted in previous studies makes it difficult to place much if any confidence in the use of ovipositor characteristics as diagnostic features for ichneumonid taxa at any level. Of particular concern are the features used by Townes (1970b) for describing the ophioniform subfamilies, the Ctenopelmatinae, and the ctenopelmatine tribe Pionini. The objective of my study is to examine ovipositor morphology across the Ctenopelmatinae to determine whether there are characteristics of the ovipositor that diagnose the subfamily and one or more of its component tribes. A related question is whether there are specific morphological details that can be used to diagnose Ophioniformes since my preliminary examination shows that the simple dichotomy of notch present or absent, as used by previous workers (see Chapter I), is inadequate.

Materials and Methods

Acquisition of Materials

Specimens used to examine ovipositor morphology were obtained initially primarily from Malaise traps operated in College Station, Texas, from 2003-2005. Additional Malaise trap material also was available from traps run in Florida, Michigan, and Idaho by D. B. Wahl, A. Cognato, and A. Gillogly, respectively. I have continued to operate Malaise traps in College Station and other localities in central Texas to acquire fresh material for dissection as needed.

Ichneumonids were removed from bulk samples and initially sorted to subfamily. Representatives of all major ophioniform subfamilies, sensu Gauld (1985) and Wahl (1991,1993a), were set aside for dissection as well as selected exemplars from outside the Ophioniformes, including some species with and without an ovipositor notch. Representatives of the following subfamilies and ctenopelmatine tribes were examined for gross morphological features: Anomaloninae, Banchinae, Ophioninae, Ichneumoninae, Tryphoninae, Diplazontinae, Campopleginae, Cremastinae, Labeninae, Pimplinae, Cryptinae, Xoridinae, Mesochorinae, Metopiinae, Tersilochinae, Orthocentrinae, and Ctenopelmatinae (Pionini, Perilissini, Euryproctini, and Mesoleiini) (Tables 2-4). Emphasis was placed on the Ctenopelmatinae for detailed character analysis. Of the ctenopelmatine samples available in alcohol for dissection, pionines and mesoleiines are best represented with seven different genera and seven species of pionines and eight genera and thirteen species of mesoleiines. Perilissines are represented by six genera and eight species. The following genera were examined from pinned specimens only, due to unavailability of material for dissection, with the number in parenthesis corresponding to the number of species examined if greater than 1: Ctenopelmatini [*Ctenopelma (2), Homaspis,* and *Xenochesis*]; Pionini sensu Townes (1970b) [*Hodostates (2), Lethades (2),* and *Pion*]; Perilissini [*Lathrolestes (12), Nanium (4), Neurogenia, Trematopygodes (2), Priopoda (2), Perilissus (5), and Alexeter (2)*]; Mesoleiini [*Anoncus (2), Barytarbes (2), Campodorus (3), Lamachus, Mesoleius (8), Neostroblia,* *Saotis,* and *Scopesis*]. These genera are in addition to the genera listed in tables 2 and 3, with genera being repeated if additional species were examined from pinned material. With the inclusion of pinned material a total of nine genera of perilissines and mesoleiines were examined with the highest number of examined species being from *Lathrolestes* and *Mesoleius*. Greater than three hundred specimens were examined.

Data Collection and Specimen Processing

Dissections were the main source of data collection regarding the characterization of ovipositor morphology. Dissections were made using a stereo microscope equipped with an ocular micrometer. Approximately 30 morphological characters were examined in detail and 25 of these were coded for selected taxa as shown in Tables 2-4. Some of these characters were chosen to verify features previously used to support either the Ophioniformes, or the Ctenopelmatinae and its included tribes. Others represent an effort to find characters useful for differentiating Ctenopelmatinae from other subfamilies. The following character systems were examined: presence, shape, and position of notch; shape of dorsal valve on either side of notch; relative length of ovipositor; fusion and alignment patterns of dorsal and ventral valves; form of basal enlargement of dorsal and ventral valves; occurrence of serrations and ridges; and arrangement of valvilli. The valvilli are articulated, chitinous flaps protruding from the lower valve into the egg canal (Quicke *et al.* 1992). Tryphonines were examined to correlate abundance and location of valvilli relative to movement of a stalked egg along the ovipositor. The term olistheter (Smith 1969) is used in several places in the descriptions below and is the tongue and groove mechanism that enables the upper and lower valves to remain connected while the ventral valves slide back and forth when penetrating the substrate and/or host (Rahman *et al.* 1998; Quicke *et al.* 1994, 1999).

Ovipositor shape has been documented through pictures produced from Automontage® software. These pictures also allow for more precise measurements regarding angles of the notch and other morphometric characters. All data, including descriptions of characters and character states, were entered into mx, a web-based data management system (Yoder 2007). Documentation of specimens in mx includes the assignment of a unique number for each of the specimens examined. Each specimen represented by an mx number will be associated with full locality information as well as collector and preliminary identification. Identifications can be refined at any time. Upon completion of each dissection, the specimen’s parts are assigned the same number as the original specimen, and kept in 80% EtOH. After dissections, voucher specimens were dried, pinned, and deposited in the Texas A&M University collection as voucher number 676.

Measurements

Specific measurements associated with the notch provide quantitative data useful for comparison of shape across taxa. These measurements include relative height of the dorsal valve and the depth and width of the notch. Relative height of the dorsal valves was measured by determining the height anterior and posterior to the notch (thus, two measurements) making sure to exclude the distance between the lowest point of the notch and the olistheter. The depth of the notch was measured as the vertical distance between the bottom of the notch and an imaginary line extending tangentially over the notch from the top of the dorsal valve. Width of the notch (Fig 19) was based on the angle from the centermost point of the notch and its tangent both anterior (Fig 19 A) and posterior (Fig 19 B) to the dorsal valve; the greater the angle, the wider the notch. Determination of angles was made by using the common sine function from trigonometry, with the tangent line forming the hypotenus of the right triangle.

Analysis of Morphological Data

The morphological data were used to address a series of specific questions. Before we can address these questions, a few definitions might be in order. The term diagnosis is used throughout the thesis to differentiate between or among different taxa. The monophyly of most of the taxa under investigation has yet to be established thus diagnostic features presented in this thesis are not necessarily synapomorphies for the taxon in question. In this chapter, a number of morphological features are described, many of these for the first time, and is characterized by two or more different states. These character states were assessed for their utility as diagnostic features for the taxa I studied. The term description refers to the list of characters,that in combination, is used to provide in this study a verbal picture of the morphological features relevant to an understanding of the taxon. Monophyly is used in its traditional sense for example as used by Wahl (1991, 1993a,b).

The first question addressed in this chapter is whether the presence of an ovipositor notch is a synapomorphy of the Ophioniformes. This was explored using Diplazontinae as an outgroup. Diplazontines are currently placed within the Pimpliformes (Wahl 1990). My preliminary dissections showed that at least some species of Diplazontinae possess a notch resembling those of banchines and mesoleiines, typical members of the Ophioniformes. By comparing various ophioniform ovipositors to those of diplazontines, I wished to determine whether there are specific morphological details that can be used to diagnose Ophioniformes, since my preliminary examination showed that the simple dichotomy of notch present or absent is inadequate.

A related question is whether there are characteristics of the ovipositor that diagnose the Ctenopelmatinae, as well as the Pionini. To answer these questions, ctenopelmatine ovipositors were compared with those of Ophioniformes (including Tryphoninae), and characteristics of the notch were examined to look specifically for evidence of transitions between the needle-like pionine ovipositor and the notched ovipositors of other ctenopelmatines. To determine whether or not a transition exists, a survey of various ctenopelmatines with special emphasis on perilissines and mesoleiines was conducted. For each available species, I measured the angles on both sides of the notch as depicted in figure 19. I looked specifically for a gradual transition between a narrow, deep notch, as exemplified by one of the species of *Perilissus* that I have seen (Fig. 20) and a broad, shallow notch as exemplified by other species of *Perilissus* (Fig. 21). This transition can be quantified by a gradual increase in angles A and B (Figure 19). An alternative hypothesis to a gradual transition to the pionine character state is that there are only two or three discrete states that characterize the ctenopelmatine notch: (1) narrow and deep, (2) broad and shallow, (3) absent. By examining material from two different ctenopelmatine tribes, I have explored whether or not there is more than one evolutionary path from the conspicuous notch to the needle like ovipositor. Both Mesoleiini and Perilissini have at least one species with a needle-like ovipositor that appears to be similar to that of pionines.

All morphological data are assembled into a data matrix for use by collaborating scientists working on the phylogeny of Ctenopelmatinae and Ophioniformes. An ancillary goal is to assemble a character by OTU matrix that can be easily incorporated into a larger morphological matrix for analyses. The primary collaborator is Jacques Dubois, who is focusing on the Pionini. The phylogenetic analysis, however, is not intended as a part of this thesis.

Results

Ovipositor Characters and Associated States

Different morphological characters associated with the ovipositor were examined and several character states defined for use in addressing the objectives. Of the 23 characters described below, 17 number have not been previously investigated. A general description of these characters and character states is provided in this section, including specific features associated with the sub-apical notch.

1 Basal Expansion

Three states characterize the basal region: (0) bulbous with an abrupt change relative to the rest of the ovipositor (Fig. 22), (1) thick when compared to the rest of the ovipositor but without an abrupt change (Fig. 23), (2) base relatively equal in height to the rest of the ovipositor.

2 Upper Margins of the Dorsal Valves Basad Notch

Four character states describe the upper margin of the dorsal valves: (0) upper margins of the dorsal valves run parallel to the olistheter, (1) margins run parallel to the olistheter then gradually decrease towards the notch (Fig. 24), (2) upper margins gradually decrease towards the notch becoming the notch, without clear demarcation between slope and notch (Fig. 25), (3) upper margin of the dorsal valves gradually decrease towards the apex of the ovipositor with an interrupted drop into the notch.

3 Upper Margin of Dorsal Valves Distad Notch

Three character states describe the condition of the upper margin of the dorsal valves posterior to the notch: (0) upper margin runs parallel to the olistheter (Fig. 26), (1) upper margin convex, tallest part in middle portion (Fig. 27), (2) upper margin convex, tallest part in basal portion (Fig. 28).

4 Structures on the Lateral Sides of the Dorsal Valves

Structures on the lateral sides of the dorsal valves are coded as presence/absence character states: (0) absent, (1) present (Fig. 29). These structures are additional to the serrations at the apex of the ventral valves (character 12) and the ridge like remnants of serrations on the dorsal valve (character 17). They also differ from a nodus in that a nodus is defined (Townes 1969) as a dorsal prominence.

5 Fusion Patterns of the Dorsal Valves

The fusion patterns in the dorsal valves are highly variable across the examined taxa. Because of this, two characters are defined, one a subset of the other. The first consists of three character states: (0) no fusion, (1) partial fusion (Figs. 30-32), and (2) complete fusion. No fusion occurs when the two dorsal valves are separate from one other and you can move each valve independently, as is typical of sawflies. When the dorsal valves form a solid unit without being separated by either a membranous area *or* a medial line they are considered to be completely fused. Partial fusion is a highly variable feature among the taxa and is treated as a separate set of characters in the next three paragraphs.

6 Partial Fusion

Partial fusion describes the presence of a median line or membranous region basally separating the two dorsal valves. Because partial fusion is highly variable, additional states are used to characterize the extent of a membrane or median line along the ovipositor: (0) separation of dorsal valves extends distally into the notch (Fig. 33A), (1) separation of dorsal valves is evident basally and distal to the notch, but not in the notch (2) membrane or median line extending through the notch and distal to the notch thus running the entire length of the ovipositor, though sometimes interrupted on distal slope of notch (32A), or (3) separation of dorsal valves present only basally, not extending through either the notch or distad.

7 Partial Fusion of Dorsal Valves at the Base

Between the base of the ovipositor and sub-apical dorsal notch, variation occurs with regard to degree of sclerotization. There are 2 character states assigned to this character: (0) desclerotization occurs in a broad V-shaped configuration with the outlines of the dorsal valves being distinctly more sclerotized (Fig. 32B), (1) desclerotization is more confined to the medial area of the dorsal valves with a gradual increase in sclerotization as you move disally along the dorsal valves (Figs. 31A & 33B).

8 Medial Structures in Desclerotized Basal Portion of Dorsal Valves

Within the area of descelerotization at the base of the dorsal valves, the dorsal valves meet along a midline that’s either: (0) membranous (Fig. 32C) or (1) variously sclerotized but not completely membranous (Figs. 31B & 33C).

9 Alignment Patterns of the Ventral Valves

The ventral valves are never fused with gaps occurring in various positions along the entire length of the ovipositor. There are two states assigned to this character: (0) gaps present along midlength, (1) gaps only at extreme base and apex. We only observed state 1.

10 Valvilli

The first character associated with valvilli is a presence or absence condition: (0) valvilli absent (Fig. 34), (1) valvilli present (Fig. 35). Valvilli are present in nearly all specimens examined, but intraspecific variation in the presence or absence of valvillae was observed for two species of Ctenopelmatinae: 1 specimen of *Campodorus* species 3 and 1 specimen of *Oetophorus pleuralis*.

11 Pairs of Valvilli

The numbers of valvilli present on the ventral valves are counted in pairs. In order to be considered a pair there is one valvillus on each valve in the same relative position. Character state 0, equals no pairs, character state 1, equals 1 pair, etc.

12 Placement of Valvilli

If valvilli are present, there are two character states assigned to the position of valvilli relative to the notch. (0) valvilli are proximal to the notch and (1) valvilli are distal to the notch. Theoretically, valvilli could also occur adjacent the notch, but I did not observe any species with this characteristic.

13 Desclerotization at the Base

Four states characterize desclerotization at the base of the ovipositor: (0) absence of desclerotization, (1) desclerotization only at the base of the dorsal valves, (2) desclerotization only at the base of the ventral valves, (3) desclerotization at the base of both dorsal and ventral valves.

14 Serrations on the Lower Valves

As noted above, serrations are often found on the apex of the lower valves, and this is treated as a simple presence/absence character: (0) serrations absent, (1) serrations present.

15 Sub-Apical Dorsal Notch

There are eight characters associated specifically with the sub-apical dorsal notch, and most of these are described in the next seven paragraphs. However, initially there are two character states: (0) absence (Fig. 13), (1) presence (Fig. 36).

16 Sub-Apical Dorsal Notch Relative to Olistheter

This character specifies whether or not the deepest portion of the notch touches the olistheter: (0) notch does not touch the olistheter (Fig. 37), (1) notch touches the olistheter, with no measurable space between the two.

17 Proximal Ridges on Downslope of the Sub-Apical Dorsal Notch

Two character states describe longitudinal ridges on the proximal, downslope of the sub-apical dorsal notch: (0) ridges absent, (1) ridges present. None of the taxa examined had ridges present.

18 Longitudinal Ridges on the Distal End of the Sub-Apical Dorsal Notch

As with the previous character, only two character states are needed to define this character: (0) ridges absent, (1) ridges present, giving the appearance of a well-defined edge (Fig. 38). Ridges are often very fine and occur on the middle rather than lateral part of the dorsal valve, as in character 19.

19 Ridges on the Apex of the Dorsal Valves

There are two states: (0) absent, (1) present (Fig. 39A). These ridges are presumed to be remnants of serrations of the dorsal valves, a character only present in basal ichneumonids (Quicke *et al.* 1994, 1999).

20 Length from Midnotch to the Apex of the Ovipositor

The length from mid notch to the apex of the ovipositor is a continuous character. Because of that, the character states are coded as whether or not the sub-apical dorsal notch is in the middle of the ovipositor or between the middle and apex of the ovipositor: (0) in the middle of the ovipositor (Fig. 39), (1) between the middle and apex of the ovipositor (Fig. 38). Although the length from mid notch to apex of the ovipositor is a continuous character, states as described here are discontinuous.

21 Relative Height of the Dorsal Valve on Either Side of the Sub-Apical Dorsal Notch

The height of the dorsal valve proximal and distal to the sub-apical dorsal notch was measured, and coded as three states: (0) height of the dorsal valve proximal to sub-apical dorsal notch is equal to the height of the dorsal valve distal to the notch, (1) height of the dorsal valve proximal to the sub-apical dorsal notch is greater than the height of the dorsal valve distal to the sub-apical dorsal notch (Fig. 40), (2) height of the dorsal valve distal to the sub-apical dorsal notch greater than the height of the dorsal valve proximal to the sub-apical dorsal notch.

22, 23 Shape of the Notch

In order to further characterize changes occur in the shape of the notch, the notch was divided into two halves, the proximal (character 22) and distal (character 23). There are four easily characterized states assigned to each character: (0) concave, (1) convex, (2) diagonal, and (3) vertical. Four intermediate states for specimens that were difficult to code. These intermediate states are: 1/0, 1/2, 2/0, 2/1.

The following characters are shared among all the subfamilies examined and therefore are not repeated in the diagnosis of subfamilies: ridges of the lateral sides of the ovipositor absent (except in Xoridinae and Labeninae); alignment patterns of the ventral valves are regular; and proximal ridges are absent on downslope of the sub-apical dorsal notch when the notch is present.

Differentiating Ophioniformes from Pimpliformes, as Represented by Diplazontinae (Tables 2 and 4)

There are no characters possessed by all members of the Ophionformes examined in this study that are not found in at least some species of Diplazontinae. All members of the ophioniform subfamilies Anomaloninae, Banchinae, Campopleginae, Cremastinae, Ctenopelmatinae, Ophioninae, and Tersilochinae examined in this study possess the following character states (Table 2): dorsal valves partially fused; valvilli present, represented by either 1 or 2 pairs; valvilli placed proximal to sub-apical dorsal notch; sub-apical dorsal notch usually present and located between middle and apex of ovipositor; and ridges absent on apex of ovipositor. With the exception of the ovipositor notch, which proved variable within Ctenopelmatine, these character states will not be repeated in the descriptions of subfamilies and tribes given below.

The diplazontine ovipositor can be described as follows: 20% of dorsal valves completely fused; valvilli arranged in 1 to 3 pairs with about 25% of the individuals examined having 1 pair, 25% having 2 pairs, and 50% having 3 pairs; apex of the ovipositor with 1 or 2 ridges in 60% of individuals examined; and valvilli distal to sub-apical dorsal notch. While most of the features listed here are too variable for use in unambiguous differentiation of diplazontine ovipositors from those of the Ophioniformes, the position of the valvilli is diagnostic relative to Ophioniformes, in which the valvilli are never distal to the notch. Additional characters found in all diplazontines examined include: base usually thick; upper margins of dorsal valves never run parallel to the olistheter; upper margins of dorsal valves distad sub-apical dorsal notch usually spade shaped; heavy desclerotization at base of dorsal valves, sometimes extending almost to the sub-apical dorsal notch; serrations usually present apically on ventral valves; and sub-apical dorsal notch usually present.

Characters States Common to Members of the Ctenopelmatinae (Table 3)

Of the seven different tribes included within the subfamily Ctenopelmatinae by Yu and Horstmann (1997), adequate material for dissection was available only for the four largest tribes: Euryproctini, Mesoleiini, Perilissini, and Pionini. Of the others, the Olethrodotini is known only from two seldom-collected Palaearctic genera (Townes 1970b), and I only had access to males. The Scolobatini (including the Westwoodiini of Zhaurova and Wharton 2009), was represented by pinned specimens of several genera, all of which had a distinct sub-apical notch that varied somewhat in width and depth among species. Only three of the six genera of Ctenopelmatini were examined, and these exhibited exceptional variability. For example, some species of *Ctenopelma* , such as *C. sanguineum* (Provancher) and *C. petiolatum* Barron have a sub-apical dorsal notch whereas other do not, such as *C. longicrus* Barron and *C. ruficeps* Barron (Barron 1981). Species of *Homaspis* do not possess a sub-apical dorsal notch but species of *Xenochesis* have a very conspicuous sub-apical dorsal notch. The Ctenopelmatini are typical of variation in all tribes that precluded definitive characterization of the ovipositor of the subfamily Ctenopelmatinae.

Pionini

A sub-apical dorsal notch was present in the ovipositors of all specimens of *Hodostates* and *Labrossyta* examined. The notch is absent in all other pionines examined, and those that were dissected all had 2 pairs of valvilli. With *Hodostates* and *Labrossyta* included, the following characters are common to all members of the tribe: base expanded, never equal in height to rest of ovipositor; both dorsal and ventral valves at least partly desclerotization.

Perilissini

Although a high degree of variability exists within Perilissini, there is a suite of characters that, when taken together, can be used as diagnostic for Perilissini relative to other ctenopelmatine tribes. These are: base never bulbous; upper margins of dorsal valves never run parallel to olistheter; the extent of partial fusion can be in the notch, both in the notch and distad notch, or neither but never simply distad notch; 88% of the time with 2 pairs of valvilli; basal desclerotization never on dorsal valves alone; and serrations present on the lower valves. Additionally, with the exception of *Perilissus* sp. 1, the notch doesn't touch the olistheter.

Mesoleiini

Members of the tribe Mesoleiini share the following combination of characters: base always thick; upper margin of dorsal valve never parallel to olistheter; upper margin of dorsal valves distad notch never spade shaped; 1 pair of valvilli; desclerotization never on dorsal valves alone; overall, dorsal valves proximad notch taller than distad notch; and distal half of notch always concave. Additionally, serrations are present on apex of ventral valves except in *Anoncus*; ridges are present on distal half of sub-apical dorsal notch, except in *Campodorus* sp. 3; and partial fusion either extending to apex or to the notch but not evident in the notch or distad the notch, except in *Mesoleius* sp. 1.

Euryproctini

The following combination of characters is found in all euryproctines: base thick; upper margins of dorsal valves proximad notch either decrease into the notch or decrease toward the notch with an interrupted drop into the notch; upper margins of dorsal valves distad notch either parallel to olistheter or spade-shaped; partial fusion extends to apex or just through the notch; 2 pair of valvilli; desclerotization present on the ventral valve or none at all; and serrations present on apex of ovipositor.

Other non-ophioniform Subfamilies (Table 4)

Members of the Ichneumoninae (2 species examined), Tryphoninae (3 species examined), Pimplinae (2 species examined), Xoridinae (2 species examined), Labeninae (1 species examined) and Cryptinae (2 species examined) all had apically serrated ventral valves and lacked a sub-apical dorsal notch. Of the species examined, ichneumonines, cryptines, mesochorines, labenines, and tryphonines all possess valvilli, although numbers are variable. Both ichneumonines and cryptines have a well developed nodus located on the apex of the dorsal valves whereas species of Xoridinae and Labeninae possess several bumps, in place of a nodus, on the apex of the dorsal valve.

Discussion

There are several morphological characters of the ovipositor that are present in all members of the Ophioniformes examined in this study. However, I did not find any characters specific to Ophioniformes that were not also present in at least some of the non-ophioniform taxa. Thus, I was unable to find support for the monophyly of the Ophioniformes sensu Gauld (1985) and Wahl (1991, 1993a), or even the expanded Ophioniformes of Quicke *et al.* (2000), Belshaw and Quicke (2002), and Quicke *et al.* (2005) using the ovipositor characteristics that I examined. More specifically, the sub-apical, dorsal notch has apparently been lost independently several times within the Ctenopelmatinae and also in the Tersilochinae. More significantly, although used previously as a defining feature of the Ophioniformes (Gauld 1985, Wahl 1991, 1993a), a well-defined notch is also present in many Diplazontinae, Orthocentrinae, and

Metopiinae. While Quicke *et al*. (2005) included Metopiinae in their expanded Ophioniformes, the Diplazontinae and Orthocentrinae remained nested deep within the Pimpliformes in the analyses by Quicke *et al*. (2000) and Belshaw and Quicke (2002), supporting the original inclusion of these subfamilies in Pimpliformes by Wahl (1990). This leaves Ophioniformes, as defined by Gauld (1985) and Wahl (1991, 1993a) without any morphological synapomorphies. Yet, members of the subfamily Diplazontinae do differ, in characters of the ovipositors from members of the Ophioniformes. These differences suggest areas of future investigation for features that might support the monophyly of the Ophioniformes. Specifically, placement of the valvilli needs to be surveyed in more detail among those non-ophioniform taxa with a sub-apical dorsal notch, such as the Orthocentrinae that were not examined in this study. The loss of serrations or ridge-like remnants apically on the dorsal valves may have occurred independently in Ophioniformes and a few non-ophioniform taxa, and this hypothesis can also be tested by a more detailed survey of ichneumonid taxa.

I also failed to find definitive characters of the ctenopelmatine ovipositor. Though disappointing, this is not surprising since Townes (1969, 1970b) noted only that the ctenopelmatine ovipositor is short and bears a sub-apical dorsal notch. Townes (1970b) also noted several important exceptions. Even if we ignore the Olethrodotini, whose two known species have exceptionally long ovipositors, ovipositor length varies considerably among the remaining Ctenopelmatinae. In some Pionini and Perilissini, the ovipositor is longer than the apical depth of the metasoma. Ovipositor length is not obviously correlated with body size since some of the shortest ovipositors are found in the

Westwoodiini, which are among the largest of the Ctenopelmatinae. In Perilissini, relatively long ovipositors are found in small-bodied *Lathrolestes* and large-bodied *Perilissus*. Variation in the presence or absence of a sub-apical notch, as suggested by Townes (1970b), proved more useful at the tribal level.

The tribe Pionini is a major obstacle for characterizing both the Ctenopelmatinae and the Ophioniformes on the basis of the presence of a sub-apical, dorsal notch. The notch is absent in all but two of the 18 pionine genera, and the lack of a notch has been used as a diagnostic character of this tribe (however, ignoring *Hodostates* and *Labrossyta*, both of which have notched ovipositors). There are two ways to look at the absence of a notch in the more typical pionines. The first is that it represents the primitive condition in ichneumonid ovipositors, similar to what is found in putative basal groups (e. g. Quicke *et al.* 2000), such as Xoridinae, Ichneumoninae, and most Pimpliformes. The second is that the absence of a notch represents a secondary loss associated, for example, with oviposition in host eggs. My data support the latter hypothesis since the entire ovipositor is strongly narrowed apically in pionines (often abruptly so) relative to most ichneumonids, and dorsal nodes and serrations, typical of xoridines, ichneumonines and most pimpliformes, are absent in pionines. More importantly, my survey of ctenopelmatine ovipositors shows several possible transitions from a notched to an unnotched condition. Specifically, these transitions have occurred within Perilissini, Mesoleiini, and Ctenopelmatini.

It is my hypothesis that the Pionini, as previously diagnosed by the possession of a needle-like ovipositor, is a polyphyletic group representing convergence from at least two different origins, the Perilissini and Mesoleiini. Measurements of the sub-apical notch in the perilissines *Perilissus* and *Lathrolestes* show a full range of variation among species: transitioning from a deep, relatively abrupt notch to a very broad, shallow indentation in which the notch is barely perceptible. This clearly demonstrates that the overall evolution from an ovipositor with a conspicuous sub-apical dorsal notch to an ovipositor without a notch can occur gradually as exemplified by the Perilissini. A more abrupt transition is represented by *Anoncus* of the Mesoleiini, a genus whose species have needle-like ovipositors. I was unable to find any mesoleiines with intermediate conditions of a broad, shallow notch, nor does Townes (1970b) indicate that any such species exist. The pionine genus *Rhorus* has an ovipositor that closely resembles that of *Anoncus* (straight vs. upcurved in other pionines, for example, and base condition being bulbous in both genera), suggesting a mesoleiine origin. Variation in such features as basal enlargement, apical serrations, and general curvature suggest different origins for other genera currently placed in Pionini. For example, *Pion, Lethades, Sympherta,* and *Trematopygus* all have ovipositors that differ from those of *Rhorus*, and at least some of these may have their origins from a perilissine or perilissine-like ancestor (see paragraph below on mesoleiine vs perilissine ovipositors).

The Ctenopelmatini represents a third potential origin, since needle-like ovipositors are of sporadic occurrence in this tribe. The exceptional variation observed just in the apical portions of Ctenopelmatini ovipositors suggests a potential wealth of informative characters for further exploration of the origins of notchless ovipositors in the subfamily Ctenopelmantinae but much work remains to be done.

Although the species of *Hodostates* and *Labrossyta* possess a sub-apical notch, Townes (1970b) used this feature to question whether either of these genera should be included in the Pionini. As it seems likely that the tribe Pionini is polyphyletic, resolution of the placement of these two genera is not as urgent as is a reassessment of the tribe as a whole. The placement of *Hodostates*, however, is addressed in the next chapter.

Members of the tribes Perilissini and Mesoleiini also proved to be quite variable, leading to difficulties in uncovering diagnostic characters for these tribes. Among characters diagnostic for the perilissines (relative to mesoleiines) is the basal pattern of desclerotization of the dorsal valve which is more extensive than it is in mesoleiines. An additional character is the number of valvilli. Of those examined, mesoleiines possess only 1 pair of valvilli, whereas perilissines usually possess 2 pairs (see also Quicke *et al.* 1992, in which one mesoleiine and two perilissines were examined). Although some members of both tribes have a straight ovipositor, many perilissines have a slightly upcurved ovipositor, similar to that of many pionines. Mesoleiines, on the other hand, can also have a downcurved ovipositor, similar to that of euryproctines, but the ovipositor is never upcurved in Mesoleiini.

Considerable information has been published on the functional significance of needle-like ovipositors, found throughout the Ichneumonoidea, but are particularly prevalent among species that oviposit in host eggs (Brajkovic *et al.* 1999; Wharton 1997). Pionines are generally thought to oviposit in host eggs (Pschorn-Walcher & Zinnert 1971, Townes 1970b) explaining the needle-like ovipositor in most species, but several species in the genus *Rhorus* oviposit through the stemmata of early instar larvae (Pschorn-Walcher and Zinnert 1971; Gauld 1988). This would explain why serrations are retained on the ventral valves in *Rhorus*, but lost in other Pionini.

By contrast, few papers have addressed the function of the sub-apical notch. The best of these is a paper by van Lenteren *et al.* (1998) that details the functional morphology of an ovipositor clip in *Leptopilina,* a eucoiline figitid parasitoid of *Drosophila*. In the species studied by van Lenteren *et al*. (1998), the host cuticle is held in a sub-apical notch by a sliding mechanism during oviposition bouts. Subsequent research revealed the presence of an homologous clip in several other figitids (Buffington *et al.* 2007). However, a similar sliding structure was not present in any of the ichneumonids that I examined, nor has any structure of this nature been described in the detailed studies on Ichneumonoidea by Quicke and his co-workers (Quicke *et al.* 1992, 1994, 1999, 2000). Boring *et al.* (2009) very recently summarized some of the functional morphology literature associated with oviposition in Hymenoptera, and speculated on the function of the sub-apical notch in Ichneumonoidea, using *Homolobus truncator* (Say), a braconid, as their model. Unfortunately, their work focuses on functions associated with eggs that undergo considerable distortion as they flow down the ovipositor tube, and is thus mostly inapplicable to ctenopelmatine ovipositors modified for the passage of large eggs that do not undergo distortion as they pass down the ovipositor. Nevertheless, the argument that the sub-apical notch in Ichneumonoidea serves as a way to hold the integument of the host during oviposition (Boring *et al.* 2009; Belshaw *et al.* 2003), similar to the function in figitids, is worth examining. Two other possible functions of the sub-apical dorsal notch are given by van Veen (1982), Quicke *et al.* (1999), and Boring *et al.* (2009). Van Veen (1982), working with *Banchus femoralis* Thomson, gives evidence that the sub-apical dorsal notch determined the depth of penetration during ovipositioning. Boring *et al.* (2009) suggests a similar function for a species of Braconidae. Quicke *et al.* (1999) additionally hypothesized that the sub-apical dorsal notch serves as a point of articulation where the tip would hinge up and aid during the egg's exit. My study of ctenopelmatine ovipositors shows the notch to be exceptionally variable among species, as indicated above. Such variation is difficult to understand in a taxon attacking eruciform hosts of larval sawflies. Instead, one would predict that the notch would be nearly identical across genera if the function is to anchor the ovipositor in the host integument during egg-laying. I offer an alternative hypothesis, that seems to correlate better with variation in the relatively large, stiff eggs of those ctenopelmatines with a notched ovipositor.

It was necessary to dissect the ovipositor in order to assess several of the character states discussed above. During these dissections, I observed that ctenopelmatine eggs were generally quite large (sometimes equal to or exceeding in diameter the diameter of the ovipositor) and usually weakly to strongly sclerotized. Similar observations have been made by Eichorn and Pschorn-Walcher (1973), Gauld (1984, 1988, 1997), Pschorn-Walcher and Zinnert (1971), Pschorn-Walcher (1967), Grahman (1953) and Quicke *et al*. (1999). In order for such large, stiff eggs to pass down the ovipositor, some distortion of the valves is essential. Since the upper and lower valves are fastened together by the olistheter along their length, this distortion has to occur dorsally and/or ventrally, rather than laterally. The presence of a notal membrane mid-dorsally, that results in partial fusion of the dorsal valves, is one way to obtain flexibility and the necessary expansion of the egg canal to accomodate large eggs (Quick *et al.* 1994). Quicke *et al.* (1994) describe some of the details of how this might function in those groups of parasitic Hymenoptera (including Ctenopelmatinae) that have this kind of membrane. Similarly, the ventral valves are not heavily sclerotized with their only point of articulation being with the olistheter. In essence, the ventral valves curve towards one another but are free hanging, which could compensate for large, solid eggs that are physically demanding. A relatively large egg cannot be extruded from the ovipositor into the host in the same fashion that has been described for *H. truncator* (Boring *et al*. 2009) and several other Hymenoptera (see Skinner and Thomson 1960) that have elastic eggs. Instead of, or in addition to an anchor in the host integument, another function of the ovipositor notch imay be as an egg guide, pushing the egg out of the ovipositor ventrally as it moves distally along the ovipositor shaft. Differences in size and shape of the egg should then be correlated with differences in the size and shape of the notch, providing a testable hypothesis. This hypothesis essentially takes an internal view of the function of the notch, focusing on the proximal side of the slope, whereas alternative suggestions have focused on the external features. The sub-apical dorsal notch results in a tapering of the dorsal valve which would guide the egg out rather than resulting in an abrupt stop for the egg.

CHAPTER III

REVISION OF *Hodostates* FOERSTER, 1869

Introduction

Foerster (1869) did not include any species when he described *Hodostates*, *Gnesia*, and 487 other genera of Ichneumonidae (Perkins 1962). This created many problems in the interpretation of ichneumonid genera, only partially solved by earlier workers such as Thomson (1883) and Viereck (1914, 1922). For the Ctenopelmatinae, most remaining problems were resolved by the works of Perkins (1962) and Townes (1970b).

Following Foerster (1869), *Hodostates* was first treated by Thomson (1883), when he described the Swedish species *H. brevis* and placed it in this genus. This is the first species to be included in *Hodostates*, and is thus the type species. Thomson (1883) used the name *Hodostatus* rather than *Hodostates*, but as explained by Perkins (1962), Thomson commonly changed the endings of Foerster's names. These alterations by Thomson have usually been regarded by subsequent workers as unjustified emendations. The genus *Hodostates* remained as a largely unstudied member of the Tryphoninae until the work of Townes (1970b).

Gnesia Foerster was eventually validated with the inclusion of *G. caliroae* Rohwer by Rohwer (1915). Townes (1945) and Townes and Townes (1951) presented an outline of a new classification of Ichneumonidae in two different catalogs to the North American species. In these works, he recognized ctenopelmatines as a distinct subfamily separate from the Tryphoninae, and included *Gnesia* in the subtribe Perilissina of the ctenopelmatine tribe Mesoleiini. In his subsequent treatment of the world genera, Townes (1970b) placed the Nearctic *Gnesia* as a junior synonym of the Palaearctic *Hodostates,* but failed to provide any details in support of this synonymy. Priority was given to *Hodostates* since Perkins (1962) discovered that *Gnesia* Foerster is a junior homonym of *Gnesia* Doubleday (a lepidopteran). Thus, *Gnesia* Foerster is not an available name, and Perkins (1962) provided a replacement name: *Esigna* Perkins 1962. Townes (1970b) included *Hodostates* in the tribe Pionini of the subfamily Ctenopelmatinae, but pointed out that the genus might be incorrectly placed here because the ovipositor has a weak sub-apical notch and this notch is lacking in typical pionines.

Townes (1970b) redescribed all the pionine genera, and provided a key for their identification. *Hodostates* runs to the last couplet in this key, where it is separated from *Lethades* Davis by length and shape of the ovipositor and sculpture of the mesoscutum. When Townes (1970b) redescribed these genera, he included only three species in *Lethades* and two in *Hodostates*, though Townes did note that he was aware of several undescribed species. Since that time, Hinz (1976, 1996a,b) revised the European *Lethades*, adding several more species, and described one additional species of *Hodostates*. Kasparyan (1998) also described a new species of *Hodostates* from Asia, and synonymized two of the European species (Kasparyan 1996).

The species of *Hodostates* have never been revised and older descriptions lack critical morphological details. Specimens with exposed ovipositors in the collection of the American Entomological Institute (AEI) provide an opportunity to examine the genus in more detail as a logical extension of the study on ctenopelmatine ovipositor morphology (Chapter II). Since the Pionini, including *Lethades*, are characterized largely on the basis of a needle-like ovipositor, a detailed revision of *Hodostates* that emphasizes ovipositor morphology is essential for understanding the relationships of this enigmatic genus. In this chapter, I present a revision of *Hodostates* based on available material while focusing on four specific questions:

1) What are the morphological features that support Townes' (1970b) treatment of *Esigna* Perkins as a synonym of *Hodostates*?

2) If *Hodostates* does not belong in the Pionini on the basis of ovipositor morphology, where should it be placed?

3) Does ovipositor morphology support the generic placement of *Hodostates schaffneri* Hinz?

4) Is there only one variable species of *Hodostates* in North America?

Materials and Methods

Material from the following institutions was examined:

AEI	American Entomological Institute, Gainesville, Florida, United States of America
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, United States of America
BMNH	The Museum of Natural History, London, United Kingdom
MZLU	Museum of Zoology, Lund University, Lund, Sweden
NHMS	Natural History Museum Senckenberg, Frankfurt, Germany
TAMU	Texas A&M University, College Station, Texas, USA
USNM	National Museum of Natural History, Washington, District of Columbia, United States of America
ZSM	The Bavarian State Collection of Zoology (Zoologische Staatssammlung München), Munich, Germany

The use of diagnosis is described in chapter II, and applies here as well. Descriptive terminology is adopted largely from Townes (1970b), with minor changes as in Wharton *et al*. (2008). In the descriptions below, measurements given for *H. brevis* Thomson and *H. rotundatus* (Davis) are means; values in parentheses are for the primary types of these nominal species. For the other two species, the values in parentheses are for the holotype, the other value is for a male paratype. Measurements were made using eyepiece micrometer as follows:

Head

Width of head was taken from frontal view at the widest point. Malar space was determined by measuring the shortest distance between the eye and the base of the mandible. Eye width and height were measured in after rotating the head posteriorly from the lateral view until the entire margin of eye was visible. This diagonal view allowed all margins of the eye to be visible to make the most accurate measurement. To insure repeatability, width was measured at the imaginary line connecting the ventral margins of the antennal sockets. Eye height was checked in all views to make sure it was accurately measured. To determine relative width of the eye compared to the temporal area of the head, three measurements were made from a lateral view. The first measurement was from the bottom of the antennal socket to the inner margin of the eye. The second measurement was from the inner to the outer margin of the eye. The third measurement was from the outer margin of the eye to the occipital carina. The sum of these measurements is the overall depth of the head. Three measurements were necessary because the difference in focal depth of the respective parts. Antennal segment count includes scape, pedicel, and flagellomeres, excluding the minute terminal segment. Length of the first flagellomere was taken from the point of indentation above the pedicel to the base of the second flagellomere. Width of the first and second flagellomeres was taken from lateral view excluding the setae. Measurements of total antennal length are approximate due to difficulty in measuring curled structures on intact specimens.

Mesosoma

Mesosoma length was measured from where the mesoscutum and pronotum meet diagonally to the middle of the base of the hind coxa. Body height was measured from the top of the scutellum to the bottom of the mesosoma. Body width was determined by measuring the distance between the tegula. Measurements of the mesosoma were used as a proxy for body size, since the size and shape of the metasoma can be variably affected by postmortem shrivelling or telescoping of sclerites and variation in the position of the head, postmortem, also affects attempts to measure overall length of head + body.

Forewing Length

Length of the forewing was measured from below the origin of the Costa to the apex of the wing.

Hind Femur

The length of the hind femur was determined by measuring from the point of attachment to trochantellus (referred to by Townes 1970b as the second trochanter), or basal margin of the femur, to the tibia. Width was measured at the midlength of the femur.

Hind tibia. Hind tibia length was measured from point of attachment to the femur, not from the indentation below the point of attachment, to furthest point of the tibia. The apical margin of the tibia is uneven, therefore the furthest point of the tibia is closest to the tibial spurs. Width was measured at midlength of the tibia.

Metasoma

The first tergite, or petiole, was measured in three different ways: 1) width of the apical margin, 2) width of the basal margin, and 3) length of the first tergite. Length was measured from an indentation just after point of attachment to the propodeum. These measurements characterizd the shape of the first tergite; for example, long and skinny or as short as wide. Difficulties arose when measuring the length in dorsal view due to its natural curvature or arch. This was solved by getting the "flattest" angle of the tergite in dorsal view then checking the length against length measured in lateral view.

Results

Hodostates Foerster, 1869

(Figs 41-56. Maps 1-4)

Hodostates Foerster, 1869: 202

> Type species: *Hodostatus brevis* Thomson, 1883; by subsequent monotypy based on inclusion by Thomson (1883).

Gnesia Foerster, 1869: 202. Preoccupied by *Gnesia* Doubleday.

> Type species: *Gnesia caliroae* Rohwer, 1915; designated by Rohwer (1915); first included species.

Hodostatus Thomson, 1883: 929. Emendation.

Esigna Perkins, 1962: 425. New name for *Gnesia* Förster.

Diagnosis

Hodostates is most readily recognized by the presence of long notauli extending as distinctly impressed grooves at least over anterior 0.75 of mesoscutum (Fig. 41), a small, basal glymma (Fig. 42), and completely areolate propodeum (Fig. 43). It differs from all other Pionini by the possession of a distinct sub-apical notch on the ovipositor in combination with an areolate propodeum. *Hodostates* also resembles certain euryproctine genera with short, areolate propodea and broader petioles, but differs in the possession of a glymma.

Description

Face densely sculptured (Fig. 44). Inner margins of eyes subparallel; not or only weakly emarginate. Clypeus separated from face by a distinct groove; flat to weakly convex in profile with apical margin not or only very weakly protruding; in frontal view apical margin varying in appearance from shallowly and evenly convex to very weakly and broadly truncate medially; uniformly rounded, never sharply impressed. Mandible not excavated basally; very gradually and evenly narrowing distally, not twisted; teeth subequal in length. Labial and maxillary palps shorter than head height. First flagellomere not or only very slightly longer than second, with 2-3 irregular rows of 6-8 placoid sensilla in lateral view, these not clustered to form a distinct tyloid. Vertex narrow in width (Fig. 45). Ocellar triangle obtuse. Occipital carinae complete, joining hypostomal carina ventrally distinctly before reaching mandible. Epomia absent. Notaulus strong, extending at least over anterior 0.75 of mesoscutum as a distinctly incised groove (Fig. 41). Dorsal end of epicnemial carinae distinctly separated from anterior edge of mesopleuron (by at least half basal width of mandible) (Fig. 46); sternaulus completely absent. Scutellum in lateral view varying from conical (Fig. 47) to more evenly rounded (Fig. 48). Pleural carina distinct, well developed throughout; u-shaped notch between lateral longitudinal carina of propodeum and metanotum variable. Propodeum areolate, with complete complement of carinae; all carinae distinctly elevated; posterior field elongate and sharply declivous. Hind coxal cavities confluent with propodeal cavity. Tarsal claws not pectinate. Fore wing areolet present, 2m-cu received near its outer corner; stigma short and broad; 1cu-a inclivous (Fig. 49). Hind wing with cu-a vertical or nearly so; first abscissa of Cu1 varying from slightly shorter to distinctly longer than cu-a (Fig. 50). First tergite stout, rugulose, dorsal profile arched; glymma small (Fig. 42), pit-like, near base, adjacent basal-median depression; dorsal median carina extending as a strongly elevated ridge at least 0.5 length of petiole (at level of spiracle) (Fig. 51), weakening posteriorly, occasionally discernible to apex; dorsal median and dorsal lateral carinae converging at base but not meeting; S1 very short, extending less than half distance to T1 spiracle. T2 without carina extending from base to spiracle; T2 and T3 lacking thyridia. Cerci short, somewhat broadly triangular, not or only weakly protruding. Ovipositor not up-curved, dorsal valve, where visible, with a deep sub-apical dorsal notch (Fig. 18).

Included species:

Hodostates brevis Thomson, 1883

Hodostates kotenkoi Kasparyan, 1998

Hodostates rotundatus (Davis, 1897)

Excluded species:

Lethades schaffneri (Hinz, 1996), new combination

Lethades n. sp. near *schaffneri*

Comments

Excluded Species

Both morphological and biological characters supported the transfer of *Hodostates schaffneri* to *Lethades.* Although the holotype of *H. schaffneri* lacks an exposed ovipositor, an undescribed Austrian female specimen almost identical to that of *schaffneri* possesses an exposed ovipositor lacking a sub-apical notch. Further, the ovipositor is thin and needle-like similar to that found in species of *Lethades*. Ovipositors of the specimens of *Hodostates* that I examined all possess, when visible, a dorsal valve with a sub-apical notch.

Additional characters that suggest the placement of *schaffneri* in *Lethades* include the relatively few placoid sensilla on the first flagellomere, profile of the propodeum more evenly rounded, dorsal median and dorsal lateral carinae of the petiole converging at base, possibly not meeting, and cerci parallel-sided and protruding. The elongate notaulus of *schaffneri* is an unusual feature, and is undoubtedly the reason why Hinz, who died before the description was published (Hinz 1996b), placed *schaffneri* in *Hodostates*. Unfortunately, the rationale for the generic assignment is not explicitly stated in the description. The notaulus varies from absent to deep, but very short, in the described species of *Lethades*. Despite the anomalous notaulus, the bulk of the characters, particularly ovipositor morphology, support the transfer of *schaffneri* from *Hodostates* to *Lethades*.

Host Records

Biological information is limited to three original records for species of *Hodostates*. Dalla Torre (1902) lists *Eriocampa umbratica* Kl. (Tenthredinidae: Allantinae) as a host of *H. brevis*, citing Thomson. However, Thomson (1883) did not list a host in his original description of this species. Instead, Thomson (1888) gives host records for *H. brevis*, that confirms data from Dalla Torre (1902). Kasparyan (1998) adds three species of *Caliroa* to the list of hosts of *H. brevis*, increasing the number of known hosts to four species. Biological information also has been supplied by Rohwer (1915) for the species he described as *G. caliroae*. Rohwer (1915) stated that this wasp was reared as a primary parasite from a host initially identified as *Eriocampoides* feeding on *Nyssa* *sylvatica*. However, Carlson (1979) corrected Rohwer's previous host record stating the true host of Rohwer's *Gnesia caliroae* is a species of *Caliroa* (Tenthredinidae: Heterarthrinae) that feeds on *Castanea dentata.* Thus, known host records are confined to the Tenthredinidae, but represent two different subfamilies, and the host larvae have unusual morphologies (woolly and slug-like in appearance) relative to the more typical caterpillar-like, eruciform larvae of the *L. schaffneri* host.

Placement of Hodostates within Ctenopelmatinae

Townes (1970b) placed *Hodostates* in the same couplet as *Lethades* at the end of his key to genera of Pionini and he implied a close relationship by placing these two genera next to one another at the beginning of his descriptions of pionine genera. Townes (1970b) provided two characters for separating *Hodostates* from *Lethades*: presence of strong notauli and possession of a sub-apical dorsal notch on the ovipositor. I focus on differences in ovipositor morphology in separating these two genera, and note that the notauli vary from absent to deeply impressed (but relatively short) in the described species of *Lethades.*

Townes (1970b) characterizes *Hodostates* as possessing a weak sub-apical notch, presumably based on examination of the primary types of Rohwer's and Davis' nominal species as well as specimens in his collection (AEI) that he labeled as an undescribed species. The ovipositor notch is visible in all of these specimens, and where the view is least obstructed, the notch is clearly deep and broad, rather than "weak" (Fig. 18). Townes (1970b) specifically questions his own placement of *Hodostates* in Pionini because of the possession of this notched ovipositor (since the sub-apical notch is typically absent in pionines). While I am confident in rejecting material with a notched ovipositor from Pionini (as otherwise described by Townes (1970b)), there are complications. The placement of *Hodostates* remains problematic because the ovipositor structure of the type species cannot be discerned. *Hodostates brevis* is a rare species, the holotypes of both *H. brevis* and *H. palustris* (Habermehl) (a synonym of *H. brevis*) are delicate, and in both specimens the ovipositor is enclosed by sheaths and also completely hidden by the subgenital plate. The use of a high-resolution x-ray computer tomography located at the University of Texas Austin, Department of Geological Sciences, may provide a non-invasive approach for potentially resolving this problem, but has thus far proven unsuccessful. There remains the possibility, therefore, that *Hodostates*, as defined by its type species, lacks a notched ovipositor and is thus distinct from species in North America that possess a distinctly notched ovipositor.

The European *H. brevis* (type species of *Hodostates*) is very similar morphologically to the North American *H. rotundatus*. The shape of the bluntly rounded clypeus and untwisted, evenly toothed mandibles with equally sized teeth is the same, both have short antennae and palps, and the arrangement of sensilla on the basal flagellomere is the same. Additional characters of potential use in supporting a close relationships between the two taxa include the elongate, distinctly impressed notauli; wing venation; propodeal declivity and areolation; size and shape of petiole and basal flange over the glymma; the glymma itself; and identical sculptural pattern on T1-T3. On the basis of these characters, I confirm Townes' (1970b) treatment of *Esigna* Perkins (=*Gnesia* Foerster not *Gnesia* Doubleday) as a synonym of *Hodostates* Foerster. Also, upon examination of the ovipositor in the lectotype of *Hodostates rotundatus* and determining that it has a well-developed notch, I can predict that *Hodostates brevis* possesses an ovipositor similar to that of *Hodostates rotundatus*. Similarities among the North American and European species of *Hodostates* further support the removal of *schaffneri* from *Hodostates* and placement in *Lethades.*

If *Hodostates* is removed from the Pionini on the basis of the possession of a distinctly notched ovipositor, the question then arises as to where it might best be placed within the Ctenopelmatinae. The tribes Ctenopelmatini, Perilissini, and Scolobatini can be eliminated from consideration. *Hodostates* lacks the metasomal features of the T2 carina and the configuration of the apical metasomal terga that characterize members of the Ctenopelmatini. *Hodostates* also lacks the deep, window-like, more posteriorly displaced glymma of nearly all perilissines, and does not have the reduced sculptural features of members of the Scolobatini. Similarly, the first flagellomere in *Hodostates* lacks the tyloid that characterizes Scolobatini, Westwoodiini, and most Perilissini. The tribe Euryproctini is characterized by the absence of a glymma, and many of the euryproctines have elongate bodies with a long, narrow petiole, as well as other features that preclude a close relationship with *Hodostates*. However, based in part on shared hosts (the tenthredinid genus *Caliroa* Costa) it is tempting to suggest that a relationship with the euryproctine genus *Hyperallus* Foerster might be worth exploring further. *Hyperallus caliroae* Viereck, the only known species, has a short, declivous, fully areolate propodeum as in *Hodostates*. The petiole is also similar, though it lacks a distinct glymma (some specimens have a weak impression. However, *Hyperallus* lacks any trace of a fore wing areolet, and this character is traditionally used to separate blocks of genera in keys to the larger tribes of Ctenopelmatinae.

Aside from an association with *Hyperallus*, the only other possibility for *Hodostates* within the existing classification of Ctenopelmatinae is as a member of the last remaining tribe, the Mesoleiini. *Hodostates* fits the characterization of Mesoleiini provided by Townes (1970b) since nearly all mesoleiines have a glymma and a notched ovipositor, and at least some have a fore wing areolet. However, very few mesoleiines have either well-developed notauli or a completely areolate propodeum, and the propodeum is generally elongate and not sharply declivous in mesoleiines. These differences, together with other morphological features commonly found in mesoleiines but not in *Hodostates*, make it difficult to find a home for *Hodostates* in the Mesoleiini. Among these other morphological features, I note especially that the clypeus is at least partially impressed and sharply margined as in many mesoleiines, the hind tibial spurs are exceptionally long, and a thyridium is often present.

Thus, where *Hodostates* fits in classification is still a problem. One solution might be to create a new tribe within Ctenopelmatinae for *Hodostates* as part of a larger revision of Pionini. However, determining a final resting place for *Hodostates* was not an objective of this thesis and given the complicated nature of the problem, I leave it for others to tackle.

Names and dates

Foerster's work was published in the 1868 volume of the Verhandlungen des Naturhistorischen Vereines preussischen Rheinlande und Westphalens. In most major works on Ichneumonidae, including Townes (1969, 1970a, b) and Perkins (1962), Foerster's work is cited as published in 1868. Yu and Horstmann (1997) give the actual date of publication as May, 1869. Both *Gnesia* and *Hodostates* are described on the same page of Foerster's (1869) publication. Townes (1970b) lists *Gnesia* first, followed by *Hodostates* in his synonymy no doubt because *Gnesia* has line precedence.

I follow Perkins (1962) in the interpretation of *Hodostatus* as an unjustified emendation by Thomson (1883) rather than as the description by Thomson as a new genus. *Hodostates* is just one of a large number of generic names whose gender was altered by Thomson for reasons that are not entirely straightforward (Perkins 1962, Townes 1969).

Key to the species of *Hodostates*.

1. Mid coxa black, hind legs dark……………….*H. kotenkoi* Kasparyan (not examined)

   Mid coxa never entirely black. Hind legs not as above, trochanter, trochantellus, femur and tibia orangish……………………………………………………………….2

2. Scutellum conically elevated. Lateral longitudinal carina of propodeum forming u-shaped depression anteriorly at junction with posterior margin of metanotum. Anterior margin of pronotum in dorsal view truncate to weakly convex. ……………
   ……………………………………………………………………….*H.brevis* Thomson

Scutellum lower, more evenly convex. Lateral longitudinal carina of propodeum not forming u-shaped depression anteriorly, continuously elevated to junction with posterior margin of metanotum. Anterior margin of pronotum in dorsal view distinctly emarginate…………………………………………………………*H. rotundatus* Davis

Hodostates brevis Thomson

(Figs. 45-47, 52-55. Maps 1, 2)

Hodostatus brevis Thomson, 1883: 929.

Hodostates brevis: Dalla Torre 1901: 307 (catalog); Fitton 1982: 40 (lectotype designation); Townes 1970b: 70 (as type species of *Hodostates*); Kasparyan 1998: 490 (updated host records).

Polyblastus palustris Habermehl 1925: 10-11.

Hodostates palustris: Kasparyan 1996: 196 (transfer to *Hodostates* and as probable synonym of *brevis*).

Diagnosis

Hodostates brevis is readily distinguished by the conically elevated scutellum (Fig. 47), which differentiates it from the North American *H. rotundatus*. The more recently described *H. kotenkoi* has darker legs, with the mid coxa black and the hind leg brown distad coxa.

Description

Body

1.33 (1.33) times longer than tall; 1.35 (1.39) times taller than wide, 1.79 (1.85) times longer than wide. Antenna about 1.1 times longer than forewing, about 2.2 times longer than mesosoma (measured on holotype of *H. palustris*).

Head

Punctation dense, finely granular, except weaker, more coriaceous on gena; uniformly pilose. Head 1.80 (1.75) times wider than face; face 0.44 (0.40) times as long as wide, moderately convex; clypeus weakly angled outwardly from face in profile, apical margin moderately convex to nearly truncate, evenly thickened but with indication of a sharp edge depending on angle of view; mandibular teeth subequal; eyes subparallel to slightly converging, 1.89 (1.83) times taller than wide; malar space in lateral view 0.11 (0.12) times eye height; eye relatively long and wide, in lateral view 0.89 (0.83) times as wide as temple; antenna with 28 (27) segments; first and second flagellomere 2.75 (2.5) times longer than wide; second flagellomere subequal in length to first.

Mesosoma

Pronotum in dorsal view relatively narrow, anterior margin truncate medially; in lateral view vertical groove distinctly rugose, the sculpture expanding to fill ventral corner, finely granular punctate anterior to vertical groove, polished, sparsely punctate, and flat posteriorly; mesoscutum densely, finely granular, densely covered with white setae, with discrete but shallow, parallel-sided notauli extending over anterior 0.5 of mesoscutum, weakening posteriorly but posterior 0.5 at least partially obscured by pin in available material; scutellum conical in profile, strongly elevated; mesopleuron polished, bare dorsad mesopleural fovea (Fig. 46), otherwise densely setose and punctate; subtegular ridge small, rounded; metapleuron coarsely rugose and convex ventrad pleural carina; distinct u-shaped groove between posterior margin of metanotum and anterior section of lateral longitudinal carina of propodeum; propodeum completely areolate (Fig. 52), areolae rugulose to sparsely punctate, nearly smooth, carinae delimiting areolae strongly elevated except apical transverse carina weaker medially, posterior field vertical (Fig. 53), sharply declivous; propodeal spiracle situated midway between pleural and lateral longitudinal carinae (Fig. 54), but connected to pleural carina by an additional spur-like carina.

Legs

Hind femur 4 (3.93) times longer than wide; hind tibia 8.92 (8.63) times longer than wide; hind femur 0.79 times as long as hind tibia; apex of hind tibia posteriorly with row of short, closely spaced setae forming a weak comb, but setae not obviously thickened.

Wings

Forewing 2.26 (2.41) times longer than mesosoma; areolet with 2rs-m and 3rs-m distinctly separate anteriorly, 3rs-m discrete but largely to entirely depigmented (Fig. 55); hind wing with 5 distal hamuli, cu-a vertical, first abscissa of Cu1 distinctly longer than cu-a, strongly inclivous; venation otherwise as in Fig. 50.

Metasoma

Petiole densely rugose punctate, T2 moderately rugulose punctate anteriorly, becoming smoother with scattered punctures posteriorly, smooth on subsequent tergites; petiole abruptly widening in apical third, apical margin 2.88 (2.77) times as wide as base; length 0.94 (1.14) times apical width; dorsal median carina sharply elevated over basal 0.6, not extending to apex; dorsal lateral carina flared near base overhanging glymma, extending posteriorly to apex; ovipositor exceptionally short, ovipositor sheath not or only barely visible beyond the small hypopygium.

Color

Body black; head black; clypeus orange to yellow orange over at least apical 0.6, black basally, with or without narrow black apical margin; scape and pedicel dark brown to brown with yellow apex; flagellum light brown to brown; mandibles orange with reddish brown base and teeth. Mesosoma black; hind corner of pronotum brownish orange; tegula light yellow; subtegular ridge orange to brownish orange. Foreleg coxa light orange, darker at base; trochanter and trochantellus light orange to orange; femur orange with light yellow apex; tibia and tarsi orange; fifth tarsomere light brown; pretarsus brown. Middle leg coxa orange with brown base; trochanter and trochantellus light orange to orange; femur and tibia orange; tarsi orange to brownish orange; fifth tarsomere brownish orange; pretarsus light to dark brown. Hind coxa dark brown, blackish at base, fading to slightly more orange brown at apex; trochanter and trochantellus orange; femur orange; tibia orange, light brown to brown apically; tarsi and pretarsus brown, fourth and fifth tarsi orange and yellow orange respectively in holotype of *H. palustris*. Metasoma brownish black to black; petiole with thin orange band apically; T2 varying from orange to extensively darkened basally and irregularly along middle, T3 and basal 0.25-0.5 of T4 reddish orange; seventh and eight tergite light orange.

Comments

Kasparyan (1996:1) transferred *palustris* to *Hodostates*, and stated that it is "closely related to *H. brevis* Thomson or its synonym." Kasparyan also added a *Hodostates brevis* det. label to the holotype of *palustris*. Yu and Horstmann (1997) include the generic transfer in their catalog, but list both *brevis* and *palustris* as separate (i. e. valid) species. Later, however, Yu *et al*. (2005) list *palustris* as a synonym of *H. brevis,* but do not provide additional information. Upon examination of both the lectotype of *H. brevis* and the holotype of *H. palustris*, I confirm the synonymy suggested by Kasparyan (1996). Apart from slight differences in coloration (or, more accurately, shades) noted in the description above, similarity in the shape of the scutellum argues most strongly for the synonymy. *Hodostates brevis* and *palustris* both possess a conically elevated scutellum, and the shape is identical in both specimens. The scutellum is rounded dorsally in other species of *Hodostates,* as well as in nearly all other ctenopelmatines. Subtle differences between the two species include the notaulus, shape of the petiole and overall size. The notaulus of Habermehl's type specimen appears more deeply impressed and extends the entire length of the mesoscutum. In Thomson's lectotype, the notaulus does not extend the entire length, but the pin through the mesoscutum obliterates more of the posterior half than it does in the *palustris* type specimen, and thus the observed differences may be an artifact of curation. Similarly, the petiole in the *brevis* lectotype flares outwardly in the last quarter of its length whereas the petiole of the *palustris* holotype appears to widen more gradually. The difference is subtle, and may in part be a reflection of the angle of view since the petiole is elevated fairly strongly towards the propodeum in the *palustris* type. Overall, the type of *brevis* is a much smaller specimen than the type of *palustris*, with the mesosoma about 1.7 mm long in the former and 2.0 mm long in the latter.

Habermehl (1925) described *palustris* on the basis of a single specimen, and specifically states that it is a male. Kasparyan (1996), who examined this specimen, also lists it as a male. However, direct comparison of the *palustris* holotype with the *brevis* lectotype suggests that both are females. The ovipositor sheath is barely visible in the lectotype of *brevis,* protruding beyond the small hypopygium. The hypopygium of the *brevis* lectotype is identical in shape and relative size to the last visible sternite in the holotype of *palustris*, but the genitalia are not visible externally in the latter. What appears to be part of the ovary is visible through the integument ventrally in the *palustris* type, providing additional support to my suggestion that the type is a female.

This species was originally described from Sweden, and this is the only locality given by Kasparyan (1998). Kolarov (1983) records it from Bulgaria, and Aubert (2000) notes the distribution of *brevis* as both Sweden and Bulgaria. Kazmierczak (1991) also records it from Austria. The holotype of *palustris* is from “Ohmoor” (Habermehl 1925), which was very likely somewhere in Hamburg, where the collector of this specimen lived.

Type Material Examined

Hodostates brevis

LECTOTYPE: SWEDEN: Lund, 1 ♀ (MZLU).

Hodostates palustris

HOLOTYPE: **GERMANY:** Ohmoor, 1♀ described as male, 27.viii.1915 [T. Meyer] (NHMS).

Hodostates rotundatus (Davis)

(Figs. 18, 41-44, 48-51, 56. Map 3.)

Trematopygus rotundatus Davis, 1897: 277 (key, original description); Cresson 1928: 24 (lectotype designation).

Gnesia rotundata: Townes 1945: 505 (catalog); Townes and Townes 1951: 330 (catalog).

Gnesia caliroae Rohwer, 1915: 220 (host record, original description); Townes 1945: 505 (catalog); Townes and Townes 1951: 330 (catalog); Townes 1970b (as synonym of *H. rotundatus,* inclusion in *Hodostates*).

Hodostates rotundatus: Townes 1970b: 70, 71 (transfer to *Hodostates*, synonymy); Carlson 1979: 584 (correction of host record for Rohwer's specimen).

Diagnosis

Hodostates rotundatus is readily distinguished from the European *H. brevis* by the lower, more evenly convex scutellum (Fig. 48). The more recently described *H. kotenkoi* has darker legs, with the mid coxa black and the hind leg brown distad coxa.

Description

Adult Female

Body.

1.31 (1.36) times longer than tall; 1.29 (1.26) times taller than wide; 1.69 (1.70) times longer than wide. Antenna about 1.0-1.2 times longer than forewing, about 2.3 times longer than mesosoma.

Head.

Punctation dense, finely granular, except weaker, more coriaceous on gena; uniformly pilose (Fig. 44). Head 1.92 (1.86) times wider than face; face 0.49 (0.50) times as long as wide, moderately to strongly convex; clypeus weakly angled outwardly from face in profile, apical margin weakly to strongly convex, evenly thickened but with indication of a sharp edge depending on angle of view; mandibular teeth subequal; eyes subparallel to slightly converging, 1.72 (1.76) times taller than wide; malar space in lateral view 0.10

(0.13) times eye height; eye relatively long and wide, in lateral view, 1.17 (no lectotype measurement) times as wide as temple; antenna with 28 (26) segments; first flagellomere 2.93 (3.5) times longer than wide; second flagellomere 2.48 (3.00) times longer than wide; first flagellomere 1.17 (1.17) times longer than second flagellomere.

Mesosoma.

Pronotum in dorsal view very narrow medially, anterior margin medially slightly emarginate; in lateral view coriaceous, vertical groove smooth to crenulate dorsally, often vertically weakly strigose anteriorad vertical groove, flat and coriaceous or more rarely polished, sparsely punctate posteriorly; mesoscutum densely, finely granular to granular-coriaceous with discrete but shallow, parallel-sided notauli extending to posterior margin of mesoscutum (Fig. 41), weakening posteriorly where they delimit very broad, shallow, median depression; scutellum evenly convex in profile, not strongly, conically elevated; mesopleuron bare, polished to partly very weakly coriaceous dorsad mesopleural fovea, otherwise densely setose and punctate; subtegular ridge varying from small, rounded to broadly ridge-like and more distinctly protruding; metapleuron coarsely rugose and convex ventrad pleural carina; distinct u-shaped groove absent between posterior margin of metanotum and anterior section of lateral longitudinal carina of propodeum, the carina continuous to anterior margin; propodeum completely areolate, areolae rugulose to sparsely punctate, nearly smooth, carinae delimiting areolae strongly elevated except apical transverse carina weaker medially, posterior field vertical, sharply declivous; propodeal spiracle situated midway between pleural and lateral longitudinal carinae, but connected to pleural carina by an additional spur-like carina.

Legs.

Hind femur 3.62 (hind legs missing on lectotype) times longer than wide; hind tibia 7.79 times longer than wide; hind femur 0.86 times as long as hind tibia; apex of hind tibia posteriorly with row of short, closely space setae forming a weak comb, but setae not obviously thickened.

Wings.

Forewing 2.13 (2.19) times longer than mesosoma; 5-6 distal hamuli; areolet with 2rs-m and 3rs-m varying from distinctly separate to fused anteriorly to form a stalked areolet, 3rs-m discrete, extensively pigmented in most specimens (Fig. 49); hind wing with cu-a vertical, first abscissa of Cu1 varying from distinctly longer to very slightly shorter than cu-a, strongly inclivous when distinctly longer, weakly inclivous when slightly shorter; venation otherwise as in Figs 49 and 50.

Metasoma.

Petiole densely granular-punctate to rugulose-punctate (Fig. 56), second tergite densely to moderately granular-punctate, becoming smoother posteriorly; third tergite occasionally moderately punctate, smooth on subsequent tergites. Petiole gradually widening, apical margin 2.43 (2.54) times wider than base; length 1.17 (1.12) times apical width; dorsal median carina sharply elevated over at least basal 0.75, occasionally reaching posterior margin as a low ridge; dorsal lateral carina flared near base overhanging glymma, extending posteriorly to apex. Ovipositor (Fig. 18) with conspicuous sub-apical dorsal notch uncharacteristic of pionines. Ovipositor sheath very sparsely setose and apically narrowed.

Color.

Head and body brownish black; clypeus yellow; scape, pedicel, and first three flagellomeres dorsally brown, ventrally yellow; flagellum otherwise light brown; mandible yellow with orangish red teeth. Mesosoma with hind corner of pronotum, tegula, and sub-tegular ridge yellow; foreleg coxa, trochanter, and trochantellus light yellow; femur, tibia, and tarsi light orange; fifth tarsomere light brown; pretarsus light brown; middle coxa light orange, darker at base; trochanter and trochantellus light orange; femur orange; tibia varies between light yellow and orange; tarsi light yellow, pale yellow, or yellow darkening to orange; fifth tarsomere brown; pretarsus brown; hind coxa brown, darker at base; trochanter and trochantellus light yellow or light orange; femur light orange or orange; tibia varies; tarsi brown with light yellow base; pretarsus brown; metasoma brown with orange apex; first tergite brownish black; apical tergites vary.

Variation

Color

Body black or brownish black with brownish red highlights on most dorsal surfaces of ridges; clypeus light yellow or yellow with brown on anterior margin sometimes with three light yellow spots along basal margin; tegula light yellow; sub-tegular ridge red orange. Foreleg coxa orange or with darker coloration at the base; femur and tibia vary from light yellow to orange; tarsi mostly light yellow and on occasion light brown band apically; fifth tarsomere yellow or orange; pretarsus brown. Middle coxa yellow, orange, or brownish black; trochanter and trochantellus light yellow, fifth tarsomere light brown; tibia light brown with brown apex, orange with brown apex, or orange with light brown base and apex; gaster varying from entirely brownish black to brown basally to more pale along lateral sides and posterior-lateral margins of tergites, these brownish orange to yellowish.

Morphological Features

Variation in morphological characters is discussed under the comments section.

Comments

Although I agree with Townes' (1970b) synonymy of *rotundatus* and *caliroae*, there are some significant differences between type material of the two. The lectotype of *rotundatus* has the following characters that differ from the holotype of *caliroae*: five distal hamuli vs. six; forewing areolet smaller, distinctly stalked, three sided vs. areolet larger, not stalked, distinctly four sided; section of forewing Cu1 between cu-a and Rs&M longer and narrower vs. shorter and thicker; hindwing with first abscissa of Cu1 longer than cu-a vs. shorter than cu-a; petiole stout, coarsely punctate, dorsal median carinae short, barely extending past spiracle, and with moderately strong dorso-lateral carinae vs. petiole less stout, longer and more slender, punctation less coarse, dorsal median carinae extending beyond spiracle, and with very strong dorso-lateral carinae; T2 punctation coarse vs. punctation less coarse. Variation in color also subtly differentiates the two. While these differences would normally be sufficient for recognition of the two as valid species, the 10 additional female specimens available for examination (see material examined section) possess combinations of the characters that bridge the morphological gap between the two. Specifically, in the series of three specimens from Ann Arbor, Michigan, two have a stalked areolet, 5 hamuli, and coarser T2 sculpture as in the lectotype of *rotundatus*, but only one of these has the shorter hind wing cu-a. The third specimen has the hind wing cu-a as in the lectotype of *rotundatus*, but the other characters as in the holotype of *caliroae*. Of the specimens from Stittsville, Ontario, two have T2 sculpture as in the lectotype of *rotundatus* and one as in the holotype of *caliroae*. All three had similar forewing areolets, that are somewhat intermediate in shape between the lectotype and the holotype. The two specimens from South Carolina are similarly variable. I therefore recognize only one variable species of *Hodostates* in North America, *Hodostates rotundatus*.

As noted above under the comments section for the genus, the ovipositor (Fig. 18) is visible in several specimens, including the holotype of *caliroae* and lectotype of *rotundatus*, and always has a distinct sub-apical, dorsal notch.

Type Material Examined

Gnesia caliroae

HOLOTYPE: USA. **VIRGINIA:** Falls Church, Hopkins No. 11381, 1 ♀, Nyssa, reared Aug. 10, 1913, Wm. Middleton (USNM).

Hodostates rotundatus

LECTOTYPE: USA. **NEW HAMPSHIRE**. 1 ♀, (ANSP).

Other material examined

CANADA. ONTARIO: Innisville, 1♀, 7-14.viii.1982, R. Wharton & W. Mason (TAMU); Stittsville, 1♀, 2.viii.1975, M. Sanborne (AEI); Stittsville, 1♀, 4.viii.1975, M. Sanborne (AEI); Stittsville, 1♀, 5.viii.1975, M. Sanborne (AEI). **UNITED STATES OF AMERICA. MICHIGAN:** Ann Arbor, 1 ♀, 8.vi.1963, H.&M. Townes (AEI); Ann Arbor, 1♀, 7.vii.1963, H.&M. Townes (AEI); Ann Arbor, 1♀, 3-16.ix.1975, M. Fitton (BMNH). **NEW JERSEY**: Moorestown, 1♀, 21.vi.1939, H. & M. Townes (AEI). **SOUTH CAROLINA:** Cleveland, 1 ♀, 30.v.1961, G. Townes (AEI); Cleveland, 1 ♀, 6.vi.1961, G. Townes (AEI).

Lethades schaffneri (Hinz) n. comb.

(Figs. 57-60. Map 1)

Hodostates schaffneri Hinz, 1996: 75 (tabular key, original description); Yu and Horstmann 1997: 448 (catalog).

Diagnosis

This species differs from other described members of the genus *Lethades* by the possession of distinctly impressed notauli extending at least over anterior 0.5 of mesoscutum. As in the new species described below, which has well-developed notauli, *schaffneri* also lacks pectinate tarsal claws. It differs from the newly described species in the more weakly sculptured surface of the propodeum and in the presence of the anterior portion of the lateral longitudinal carina.

Description

Body (Fig. 57)

Mesosoma 1.36 (1.34) times longer than tall; 1.20 (1.33) times taller than wide, 1.64 (1.78) times longer than wide. Antenna about 1.2 (1.05) times longer than forewing, about 2.6 (2.4) times longer than mesosoma.

Head

Sculpture finely granular matte (Fig. 58) except apical 0.7 of clypeus sparsely and deeply punctate, weakly transversely strigose to smooth not granular matte, face more densely, less finely sculptured; head 1.78 (2.03) times wider than face; face 0.53 (0.5) times as long as wide with little to no convexity; clypeus elliptical, weakly angled outwardly from face in profile, apical margin moderately convex; mandible not excavated basally, very gradually and evenly narrowing distally, not twisted, teeth subequal in length; eyes weakly converging ventrally; eye 1.86 (1.70) times as long as wide; malar space in lateral view 0.10 (0.11) times eye height; eye relatively long and wide, in lateral view, 0.95 (1.10) times as wide as temple; antenna with 36 (34) segments; first flagellomere 3 (3.2) times longer than wide; second flagellomere 2.12 (2.5) longer than wide; first flagellomere 1.38 (1.28) times longer than second; first flagellomere with 2-3 placoid sensilla in lateral view; maxillary palps nearly equal in length to height of head; occipital carina complete, joining hypostomal carina ventrally just before reaching mandible; ocellar triangle not equilateral, posterior ocelli more widely spaced.

Mesosoma

Pronotum in dorsal view narrow, anterior margin broadly truncate to very weakly, broadly emarginate medially, transverse groove smooth; pronotum laterally finely matte rugulose, including vertical groove, epomia absent, posterior margin crenulate; mesoscutum very finely matte punctate, densely covered with white setae, with discrete, relatively strong notauli extending at least over anterior 0.5 (obliterated by pin over posterior 0.5), apparently weakly converging; scutellum of holotype somewhat conical in profile, though not as strongly elevated as in *H. brevis*, more rounded in male paratype, densely granular matte on sloped surfaces posteriorly and laterally; mesopleuron bare (Fig. 59) dorsad mesopleural fovea except along dorsal margin adjacent wing, bare area partially smooth, mesopleuron otherwise very finely matte rugulose; subtegular ridge neither strongly elevated nor broad; epicnemial carina well developed, dorsal end distinctly separated from anterior edge of mesopleuron (by at least half the basal width of mandible); metapleuron very finely matte above to matte rugulose below, convex; broad v-shaped groove between posterior margin of metanotum and anterior section of lateral longitudinal carina of propodeum; propodeum weakly rugulose, rounded in profile, areolate, with anterior fields distinctly longer than small posterior fields, basal transverse carina completely absent or present only as very short connection medially between narrowly separated, very strongly elevated median longitudinal carinae, propodeal spiracle situated approximately midway between pleural and lateral longitudinal carinae, connected to pleural carina by an additional spur-like carina in male paratype but not holotype.

Legs

Hind femur 4.53 (4.17) times longer than wide; hind tibia 9.67 (11) times longer than wide; hind femur 0.78 (0.76) times as long as hind tibia; apex of hind tibia posteriorly with row of short, closely spaced setae forming a weak comb, but setae not obviously thickened; tarsal claws not pectinate.

Wings

Forewing (2.27) times longer than mesosoma; 8 distal hamuli; areolet with 2rs-m and 3rs-m meeting anteriorly, usually forming a short, broad stalk; 3rs-m a well-developed tubular vein with bullae at anterior and posterior ends in holotype but only posteriorly in male paratype; hind wing with cu-a vertical, first abscissa of Cu1 strongly inclivous, about 3 (about 2) times longer than cu-a; venation otherwise as in Fig. 57.

Metasoma

Petiole densely matte punctate, T2 finely sculptured, T3 more finely so; petiole moderately convex in profile in holotype, abruptly arched basally, nearly flat apically in male paratype, apical margin 2.53 (2.79) times as wide as base; length 0.95 (0.89) times apical width, dorsal median carinae obscured by wing in holotype but apparently very weakly developed, strongly elevated medially in male paratype (Fig. 60), weaker posteriorly but distinct to posterior margin, dorsal lateral carina extending to posterior margin but disconnected medially with basal portion ending dorsad posterior end of spiracle and distal portion beginning some distance ventrad spiracle, without flange-like expansion over glymma subbasally; glymma subbasal, wide, shallow, open distally; ovipositor not exposed; ovipositor sheath densely setose ventrally and apically, sparsely setose medially nearly bare dorsally, very gradually expanded distally, nearly parallel-sided, truncate apically; male subgenital plate emarginate, apical margin with narrow, u-shaped notch medially; cercus cylindrical, protruding, at least twice longer than wide.

Color

Body black. Head black; scape and pedicel brownish black; first flagellomere basally light brown; flagellum brown; mandibles dark brownish orange to reddish brown, basally black, apically brown. Mesosoma black; tegula brownish black, outer margins brown. Foreleg orange; coxa, trochanter and pretarsus brownish black; trochantellus brownish orange; tarsi gradually darkening distally. Middle coxa black; trochanter black, brownish orange apically; trochantellus brownish orange; femur orange; tibia brownish orange; tarsi brown. Hind coxa black; trochanter black; trochantellus orangish black; femur orange, apically brown; tibia orange with brown base and apex; tarsi brown; pretarsus brown. Metasoma black; apical half of petiole, all of T2, T3 and extreme base of T4 medially orange.

Male colored as female except: Scape and pedicel inner margins light brown, first flagellomere brown. Foreleg trochanter brown, femur brownish orange. Hind trochantellus brownish orange with black base, tarsi brown with light yellow banding basally. Petiole with orange apex, T2 and T3 orange with black medially extending over anterior 0.5, fourth tergite basally orange.

Comments

Host Records

Schaffner *et al.* (1994) reared the species subsequently described as *Hodostates schaffneri* from larvae of *Rhadinoceraea nodicornis* Konow (Tenthredinidae:

Blennocampinae) feeding on *Veratrum album* L. Schaffner *et al.* (1994) suggests that *H. schaffneri* is exclusively parasitic on *R. nodicornis*. This host has typical, caterpillar-like eruciform larvae unlike the hosts of *Hodostates*. However, since the ovipositor is needle-like, the host stage attacked is likely to be the egg.

Classification

The two Austrian specimens described below, consisting of 1 female and 1 male, are almost identical to the type material of *schaffneri*. Differences between the Austrian specimens and *schaffneri* include subtle changes in color and size, as well as sculpture. The Austrian female specimen has an exposed ovipositor similar in morphology to that of *Lethades*. It is on this basis that I transfer *schaffneri* to *Lethades*, rather than retain it in *Hodostates*. Supporting characters for the transfer include the exposed ovipositor sheath and relatively long, protruding cercus. The transfer to *Lethades* is not without problems, because most species of *Lethades* (including the type species) have pectinate tarsal claws, and in other described species of *Lethades*, the notaui are either absent or deep but very short.

Type Material Examined

Hodostates schaffneri

HOLOTYPE: SWITZERLAND. Chasseral, 1 ♀, emerged 27.iii.1992 from *Hypargyricus nodicornis* Knw. (Tenthred), R. Hinz (ZSM).

PARATYPE: SWITZERLAND. Chasseral, 1♂, emerged 23.iii.1992 from *Hypargyricus nodicornis* Knw. (Tenthred), R. Hinz (ZSM).

Lethades n. sp.

(Fig. 61. Map 1)

Diagnosis

This new species differs from other members of the genus *Lethades*, with the exception of *L. schaffneri*, by the possession of distinctly impressed notauli extending at least over anterior 0.5 of mesoscutum. As in *schaffneri*, this new species also lacks pectinate tarsal claws. It differs from *schaffneri* in the more heavily sculptured propodeum lacking the anterior portion of the lateral longitudinal carina.

Description

Body

Mesosoma 1.35 (1.37) times longer than tall, 1.45 (1.33) times taller than wide, 1.96 (1.83) times longer than wide. Antenna about 1.1 (1.0) times longer than forewing, about 2.6 (2.1) times longer than mesosoma.

Head

Sculpture as in *schaffneri* except clypeus smoother, not as deeply punctate nor strigose; head 1.94 (2.30) times wider than face; face 0.47 (0.49) times as long as wide with little to no convexity; clypeus elliptical, weakly angled outwardly from face in profile, apical margin moderately convex; mandible as in *schaffneri*, with lower tooth very slightly larger than upper (harder to determine in *schaffneri*); eyes weakly converging ventrally; eye 1.6 (1.77) times longer than wide; malar space in lateral view 0.15 times eye height; eye relatively long and wide, in lateral view, 1.06 (1.0) times as wide as temple; antenna with 33 (35) segments; first flagellomere 2.17 (3.17) times longer than wide; second flagellomere 2.17 (2.5) times longer than wide; first flagellomere 1 (1.26) times longer than second, sensilla as in *schaffneri*; occipital carina and ocellar triangle as in *schaffneri*.

Mesosoma

Pronotum in dorsal view narrow, anterior margin very weakly, broadly emarginate medially, transverse groove smooth; pronotum laterally finely granular matte, including vertical groove, epomia absent, posterior margin crenulate; mesoscutum very finely matte punctate, densely covered with white setae, with relatively strong notauli extending as discrete grooves over anterior 0.66 then converging into broad, very shallow, median depression posteriorly; scutellum as in paratype of *schaffneri*; mesopleuron, including prepectal carina as in *schaffneri* except sculpture finer, less rugulose, subtegular ridge elevated; metapleuron distinctly matte to matte punctate, convex; propodeum with surface polished between parallel-sided portion of median longitudinal carinae, otherwise granular matte, rounded in profile, areolate with pattern of smaller posterior fields similar to that of *schaffneri* but without median portion of basal transverse carina and portion of lateral longitudinal carina anterior to apical transverse carina also absent; propodeal spiracle connected to pleural carina by an additional spur-like carina in holotype but not male paratype, otherwise separate from pleural carina.

Legs

Hind femur 3.63 (4.1) times longer than wide; hind tibia 8.30 (10.1) times longer than wide; hind femur 0.70 (0.71) times as long as hind tibia; legs otherwise as in *schaffneri*.

Wings

Forewing approximately 2.19 times longer than mesosoma, 6 distal hamuli; areolet broadly open in holotype, with 3rs-m represented only by short, depigmented spur posteriorly, closed in male paratype with 2rs-m and 3rs-m converging to form a narrow, discrete stalk; hind wing with cu-a vertical, first abscissa of Cu1 strongly inclivous, about 2 times longer than cu-a in holotype, cu-a very short in male paratype, with distal abscissa of Cu1 arising near anal vein, venation otherwise as in Fig. 49.

Metasoma

Petiole densely matte punctate, T2 densely matte punctate anteriorly in holotype (weakly sculptured in male paratype), becoming more finely sculptured posteriorly, subsequent tergites polished; apical margin of petiole 3.15 times as wide as base, length 0.90 times apical width, dorsal median carinae weak, barely perceptible over basal 0.5 in holotype, slightly more visible in male paratype, dorsal lateral carina extending to posterior margin, not interrupted, not expanded basally over glymma; glymma and ovipositor sheath as in *schaffneri*; ovipositor exposed, needle-like, lacking a sub-apical dorsal notch (Fig. 61), similar in morphology to that of other described species of *Lethades* (Fig. 62); male subgenital plate emarginate, but details difficult to see; cercus as in *schaffneri*.

Color

Body black. Head black; scape dark brown, pedicel and flagellum brown; mandibles dark orangish brown with brown teeth. Mesosoma black; tegula light yellow. Foreleg orange; coxa and pretarsus brownish black. Middle coxa brownish black; trochanter brownish orange, trochantellus, femur, and tibia orange; tarsi orange with brown spotting; fifth tarsomere and pretarsus light brown. Hind coxa brownish black; trochanter and trochantellus orange with basal half of trochanter brownish black; femur orange; tibia orange, apically brown; tarsi light brown; pretarsus brown. Metasoma brownish black; T2 through basal half of T4 orange.

Male colored as female except: Mandibles orange with reddish brown teeth. Hind corner of pronotum brown, sub-tegular ridge orange with red edges. Foreleg trochanter basally brown apically orange, tibia light orange. Middle coxa brown, trochanter brown, fifth tarsomere orange. Hind trochanter brown, trochantellus orange, tarsi and pretarsus brown. Metasoma T1, T4, and all subsequent tergites brownish black.

Type Material Examined

Lethades n. sp.

HOLOTYPE: AUSTRIA: Lower Austria, Semmeringgebeit, Reichenau Distr, 26.v.1957. R. B. Benson. B. M. 1957-549. 1 ♀, (BMNH).

PARATYPE: AUSTRIA: Lower Austria, Semmeringgebeit, Reichenau Distr, 26.v.1957. R. B. Benson. B. M. 1957-549. 1♂, (BMNH).

Comments

The overall similarity of this new species and *schaffneri* enables us to predict that the ovipositor in *shaffneri* is needle-like and lacks a sub-apical dorsal notch. The needle-like ovipositor forms the primary basis for removal of *schaffneri* from *Hodostates*. I provisionally place both species in *Lethades,* though an alternative is to describe a new genus to contain these enigmatic species.

It is possible that this new species is simply a variant of *schaffneri,* since the two are so similar. Since so little material is available for study, and there are distinct differences in sculpture of the metapleuron and propodeum as well as in color, I have elected to describe this as a new species.

CHAPTER IV

CONCLUSIONS

This thesis provides a detailed study of ovipositor morphology in Ichneumonidae, with emphasis on the Ctenopelmatinae. This research has enabled me to assess evolutionary patterns across many taxonomic levels. I also have discovered that the ctenopelmatine ovipositor is much more variable than has been appreciated in the past.

Research failed to show support for the monophyly of Ophioniformes sensu Gauld (1985) and Wahl (1991, 1993a). Morphological characters previously used to unite the group were found among non-ophioniform subfamilies, such as the Diplazontinae. Therefore, Ophioniformes (Gauld 1985; Wahl 1991, 1993a) is currently left with no morphological synapomorphies, though my work points to some ovipositor characters that would be worth pursuing in this regard.

My work led to the conclusion that the Pionini, as defined by Townes (1970b) is likely polyphyletic. Townes (1970b) previously recognized Pionini as being problematic within Ctenopelmatinae, but failed to offer a resolution. I undertook a revision of the genus *Hodostates* Foerster 1869 as an initial step in resolving this problem.

The generic revision of *Hodostates* Foerster, 1869 allowed for a comprehensive comparison of the Nearctic and European species, that had never been done. Based on ovipositor morphology, *Hodostates schaffneri* Hinz, 1996 was transferred to the genus *Lethades* Davis.

Previous work on ovipositor morphology shows that there are several character systems worthy of further investigation, in addition to the characters that I examined. Most notable are the sperone, as examined by Quicke *et al.* (1999), ctenidia (Austin & Browning 1981 and Rahman *et al.* 1998), and features more specific to the olistheter and valvilli. Further examination of these characters would necessitate extensive scanning electron microscopy (SEM) or similar techniques, but might provide answers to some outstanding questions left by this thesis.

As with other research, there are many questions that remain unanswered. One of these, highlighted by Boring et al. (2009), is the functionality of large numbers of valvilli found in some taxa. Although this thesis adds to the growing information about valvilli, most notably in the works of Quicke *et al.* (1992) and Rahman *et al.* (1998), the need for such large numbers of valvilli is still completely unknown. Are high numbers of valvilli necessary for ovipositing subsequent eggs? If not, what is the purpose of having more than one pair?

A potentially much larger question for the ctenoplematines that I examined is the nature and role partial fusion plays throughout the duration of oviposition. I am in agreement with Quicke *et al.* (1994) that the function of the divided upper valve is to allow necessary distortion to accommodate larger egg sizes. Quicke *et al.* (1994) also acknowledges the limitations placed on whether or not the ovipositor can distort based on host habitat. For example, a parasitoid attacking a concealed host is less likely to have an ovipositor that allows distortion, and on the contrary would require valves with thicker walls. It would be informative to look at correlation between degree of partial fusion and its associated sclerotization patterns with the nature of its host's integument.

Lastly, it would be productive to examine the extent of oviposition penetration through the host cuticle. This research would be an expansion of van Veen's (1982) research in which he examined *Banchus femoralis* Thomson in thorough detail. However, difficulties placed on this inquiry would be the opportunity to observe and manipulate live endoparasitoids, clearly not an easy task. Answers to this and the other questions posed above would not only be beneficial to an improved understanding of ctenopelmatines, but for all Ichneumonoidea.

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APPENDIX A

FIGURES

Figs. 1 Ovipositor possessing a deep and conspicuous sub-apical dorsal notch, left lateral view. *Perilissus discolor* (Cresson, 1864).

Fig. 2 Ovipositor possessing a deep and conspicuous sub-apical dorsal notch, left lateral view. *Priopoda* Holmgren, 1856.

Fig. 3 Ovipositor possessing a deep and conspicuous sub-apical dorsal notch, left lateral view. *Lathrolestes* Foerster, 1869.

Fig. 4 Ovipositor possessing a deep and conspicuous sub-apical dorsal notch, left lateral view. *Nanium* Townes, 1967.

Fig. 5 Ovipositor with a broad and shallow sub-apical dorsal notch, left lateral view. *Lathrolestes* Foerster, 1869.

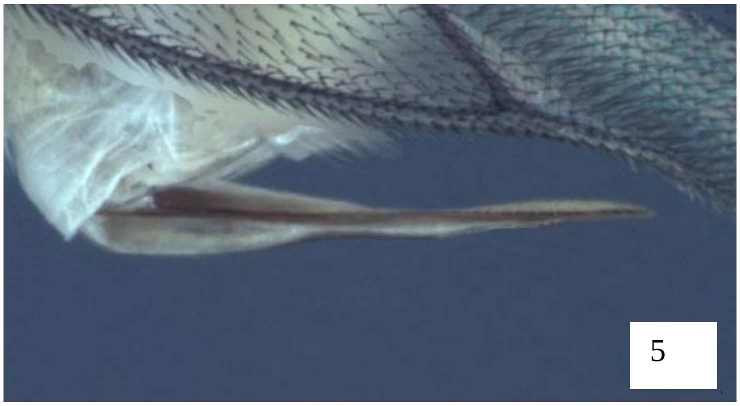


Fig. 6 Ovipositor with a broad and shallow sub-apical dorsal notch, left lateral view. *Lathrolestes* Foerster, 1869.

Fig. 7 Ovipositor with a broad and shallow sub-apical dorsal notch, left lateral view. *Perilissus coloradensis* (Ashmead, 1896).

Fig. 8 Ovipositor with a broad and shallow sub-apical dorsal notch, left lateral view. *Lathrolestes* Foerster, 1869.

Fig. 9 Ovipositor, left lateral view. *Trematopygodes* Aubert, 1968 with a broad sub-apical dorsal notch.

Fig. 10 Ovipositor, left lateral view. *Lathrolestes* Foerster, 1869.

Fig. 11 Ovipositor, left lateral view. *Lathrolestes* Foerster, 1869.

Fig. 12 Ovipositor, left lateral view. *Anoncus* Townes, 1970.

Fig. 13 Ovipositor lacking a sub-apical dorsal notch, lateral view. *Pion fortipes* (Gravenhorst, 1829).

Fig. 14 Ovipositor lacking a sub-apical dorsal notch, lateral view. *Lethades* Davis, 1897.

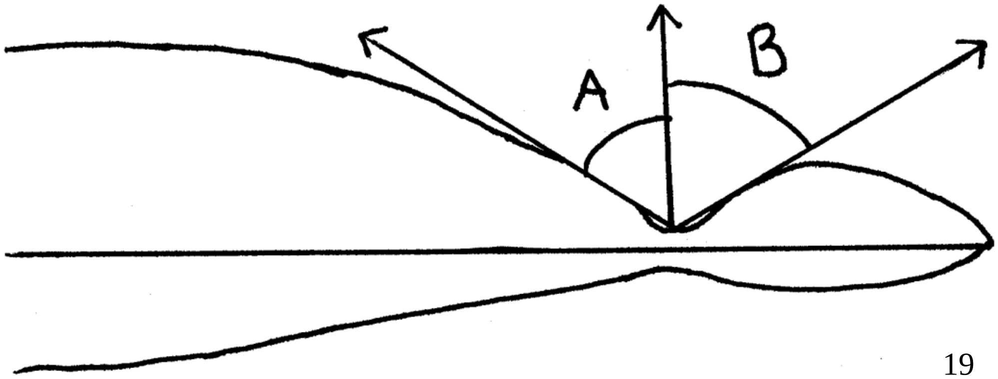
Fig. 15 Ovipositor lacking a sub-apical dorsal notch, lateral view. *Trematopygus* Holmgren, 1857.

Fig. 16 Ovipositor lacking a sub-apical dorsal notch, lateral view. *Lethades* Davis, 1897.

Fig. 17 Ovipositor, left lateral view. *Labrossyta* Foerster possessing a deep sub-apical dorsal notch.

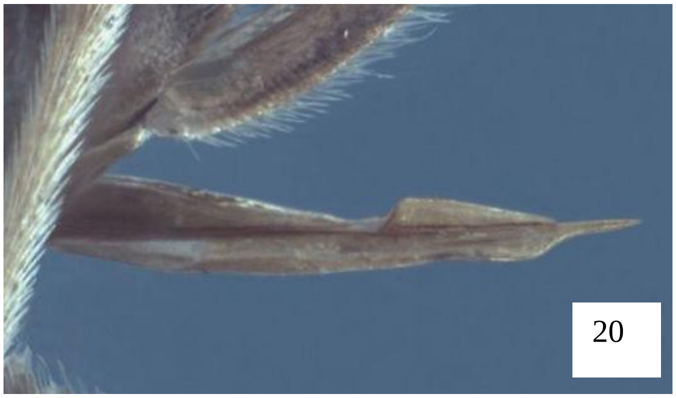
Fig. 18 Ovipositor, left lateral view. *Hodostates rotundatus* (Davis, 1897), lectotype with a conspicuous sub-apical dorsal notch.

Fig. 19 Ovipositor, left lateral view. Generalized ovipositor illustrating how angles are measured.



19

Fig. 20 Ovipositor, left lateral view. 20. *Perilissus bicolor* (Cresson, 1864).



20

Fig. 21 Ovipositor, left lateral view. *Perilissus* Foerster, 1855.

Fig. 22 Ovipositor, left lateral view. *Sympherta Foerster*, 1869, showing bulbous basal expansion with an abrupt change relative to the rest of the ovipositor (arrow).

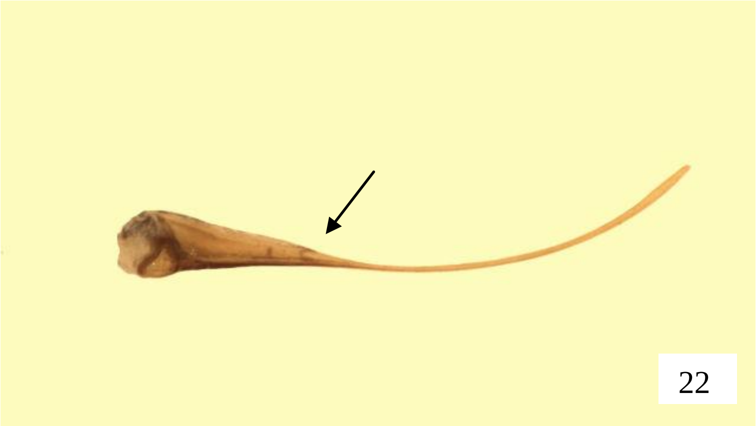
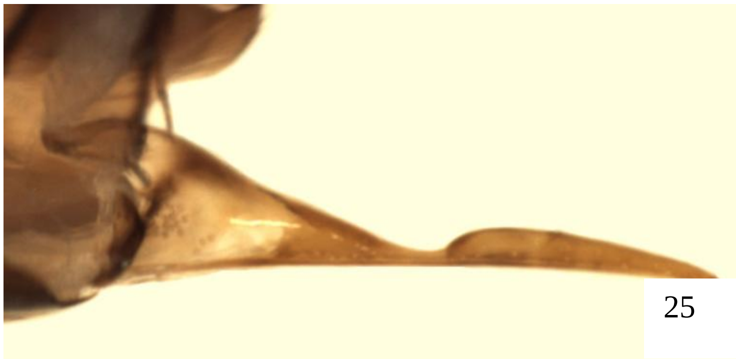


Fig. 23 Ovipositor, left lateral view. Mesoleiini species 4, showing thick basal expansion without an abrupt change relative to the rest of the ovipositor (arrow).

Fig. 24 Ovipositor, lateral view. Perilissini, upper margins of dorsal valves running parallel to the olistheter.

Fig. 25 Ovipositor, lateral view. Diplazontinae, upper margins of dorsal valves gradually decreasing and becoming the sub-apical dorsal notch.



25

Fig. 26 Ovipositor, lateral view. Diplazontinae, upper margins of dorsal valves distad sub-apical dorsal notch running parallel to olistheter (arrow).

26

Fig. 27 Ovipositor, lateral view. C*ampodorus* species 3, upper margins of dorsal valves distad to sub-apical dorsal notch taller in the middle when compared to the proximal and distal height (arrow).

Fig. 28 Ovipositor. Diplazontine, upper margin of dorsal valves distad to sub-apical dorsal notch spade shaped, lateral view.

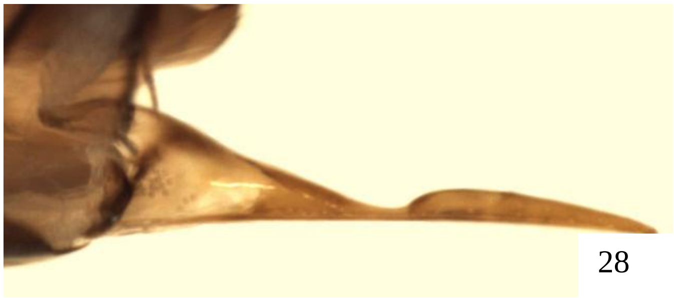


Fig. 29 Ovipositor: Xoridinae, showing structures located on the lateral sides of the dorsal valves.

29

Fig. 30 Ovipositor. *Sympherta* Foerster, 1869, showing partial fusion of the dorsal valves, dorsal view.

30

Fig. 31 Ovipositor. Mesoleiini species 3, desclerotization confined medially with a gradual increase in sclerotization as you move distally (A) and dorsal valves meeting along a sclerotized midline (B), dorsal view.

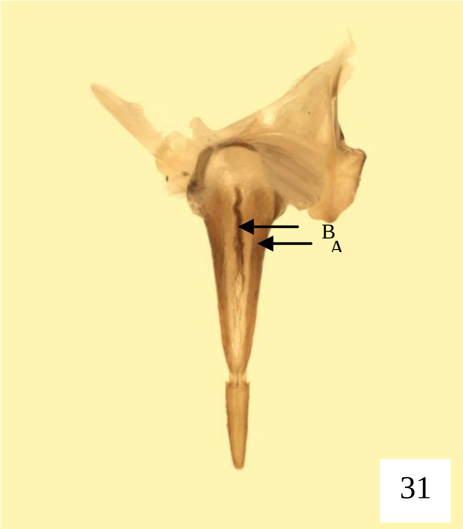


Fig. 32 Ovipositor. *Oetophorus* Foerster, 1869, showing a median line extending the entire length of the ovipositor (A), desclerotization occurring in a broad V-shaped configuration with outlines of dorsal valves distinctly sclerotized (B), and dorsal valves meeting along a membranous midline (C), dorsal view.

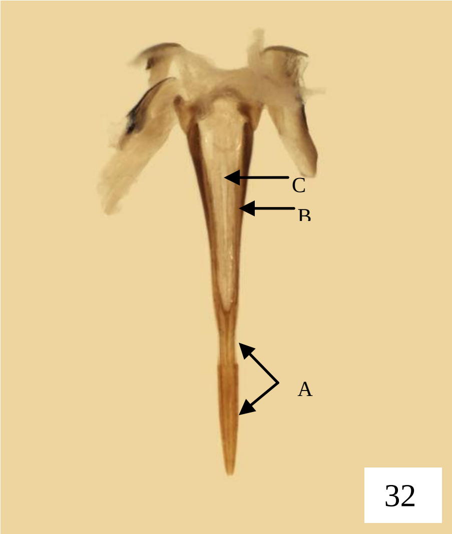


Fig. 33 Ovipositor. *Campodorus* species 2, showing a median line not extending past the sub-apical dorsal notch (A), desclerotization confined medially with a gradual sclerotization as you move distally (B), and dorsal valves meeting along a sclerotized midline (C), dorsal view.

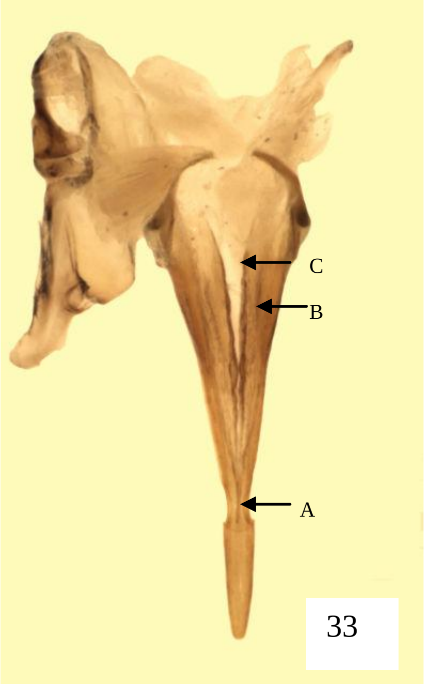


Fig. 34 Ovipositor. *Alexter* species 1, valvilli absent, lateral view.

Fig. 35 Ovipositor. *Oetophorus,*valvilli present (arrow), lateral view.

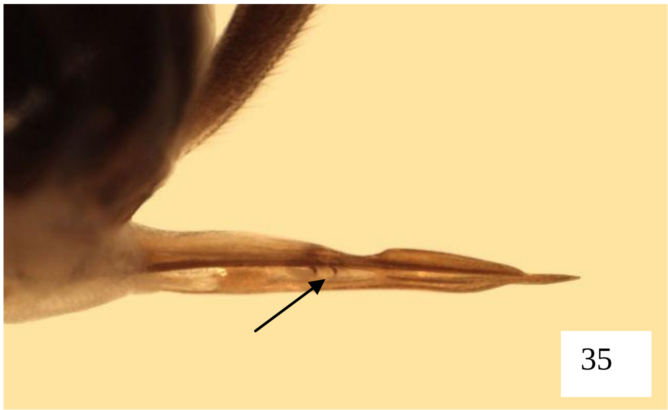


Fig. 36 Ovipositor, lateral view. *Mesoleius aulicus* (Gravenhorst, 1829), showing a conspicuous sub-apical dorsal notch (arrow).

Fig. 37 Ovipositor, lateral view. *Trematopygodes* Aubert, 1968, showing the sub-apical dorsal notch not touching the olistheter (arrow).

Fig. 38 Mesoleiini species 3, with placement of sub-apical dorsal notch between middle and apex of the ovipositor and ridges on distal end of sub-apical dorsal notch giving the appearance of a well defined edge (arrow).

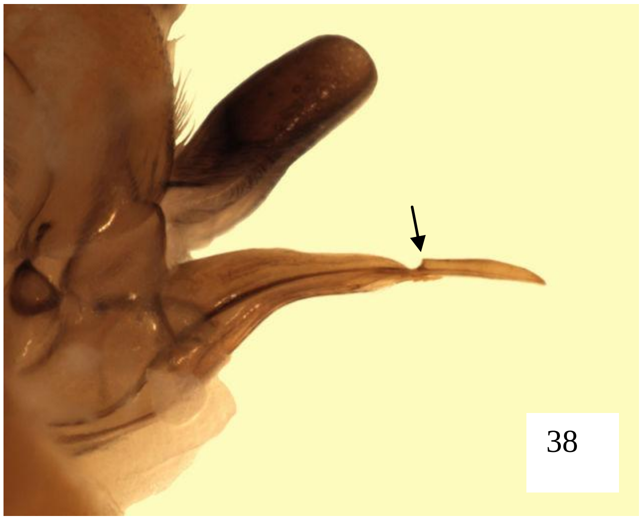


Fig. 39 Ovipositor, lateral view. Diplazontine, with sub-apical dorsal notch located in the middle of the ovipositor and with ridges located on the apex of the dorsal valves (A).

Fig. 40 Ovipositor, lateral view. *Campodorus* species 1, showing the height of the dorsal valves proximal to the sub-apical dorsal notch being greater than the height of the dorsal valves distal to the sub-apical dorsal notch.

Fig. 41 Holotype *Gnesia caliroae* Rohwer, 1915, mesoscutum with distinct notaulli extending at least over 0.75 (arrow).

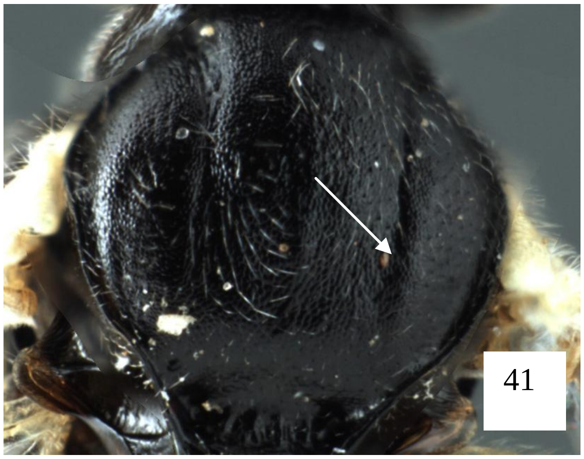


Fig. 42 Lectotype *Trematopygus rotundatus* Davis, 1897, with small glymma (arrow).

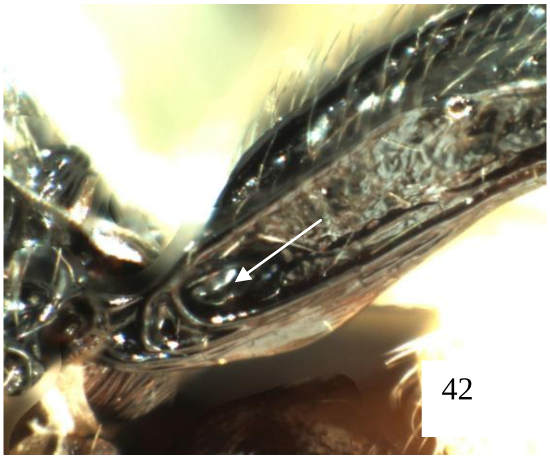


Fig. 43 *Gnesia caliroae* holotype, completely areolate propodeum.

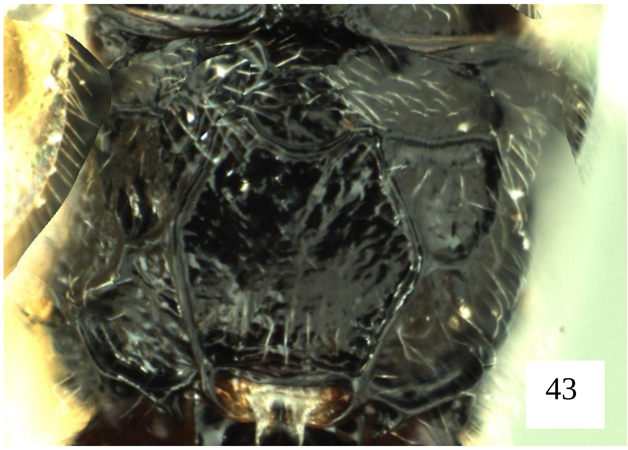


Fig. 44. *Trematopygus rotundatus* lectotype, face densely sculptured.

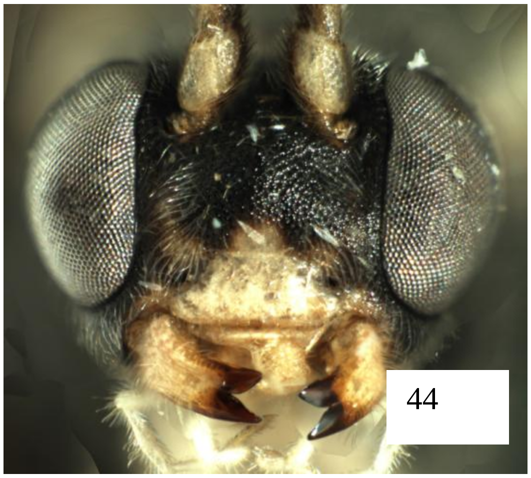


Fig. 45 Holotype *Polyblastus palustris* Habermehl, 1925, top of head.

Fig. 46 *P. palustris* holotype, mesopleuron polished and bare with epicnemial carinae not extending to anterior edge.

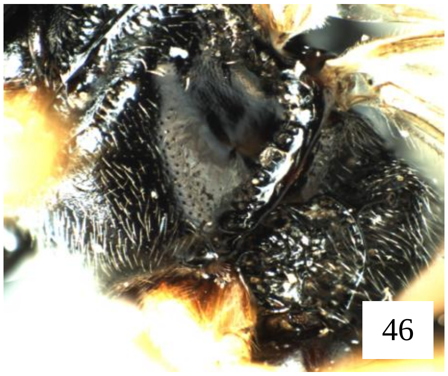


Fig. 47 *Polyblastus palustris* holotype, scutellum elevated conically (arrow).

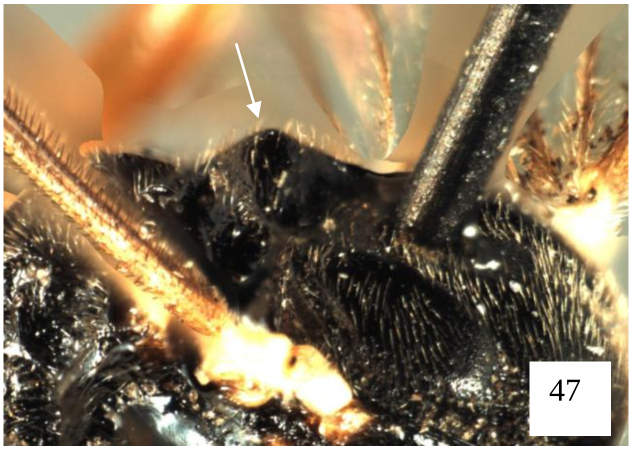


Fig. 48 Holotype *Gnesia caliroae* Rohwer, 1915, scutellum more evenly rounded (arrow).

Fig. 49 Forewing terminology. Holotype *Gneisa caliroae* Rohwer, 1915.

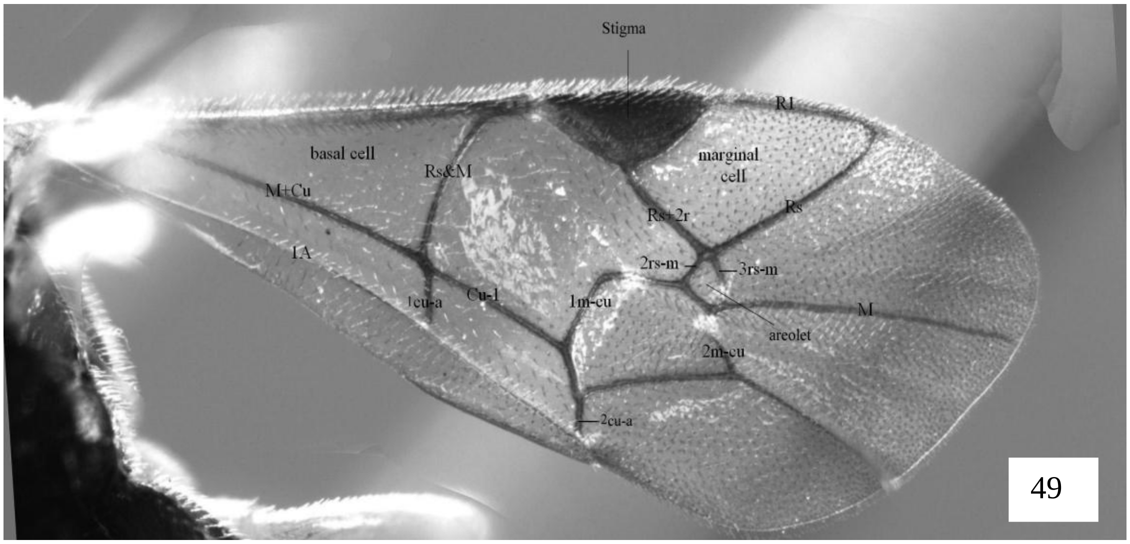


Fig. 50 Hindwing terminology. Holotype *Gnesia caliroae* Rohwer, 1915.

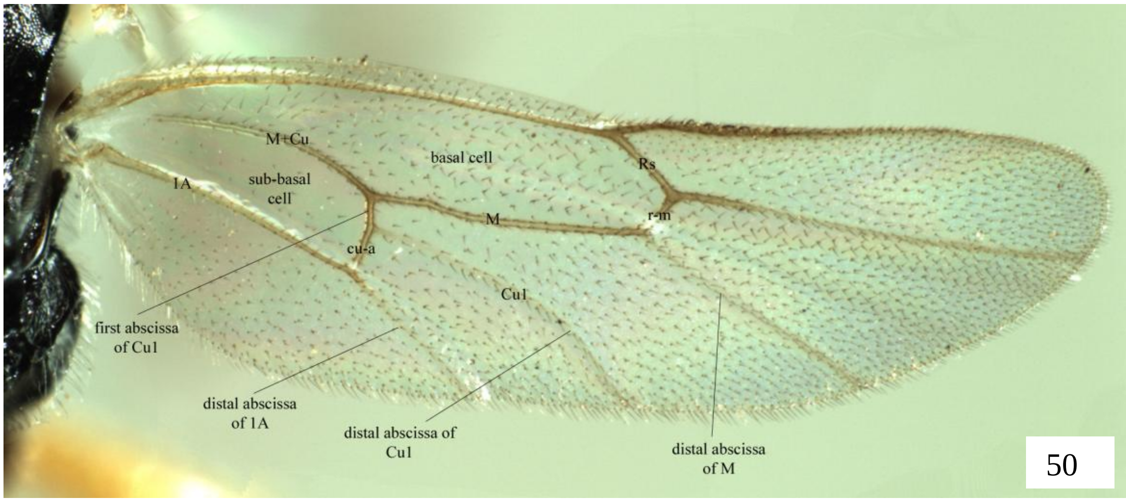


Fig. 51 Holotype *Gnesia caliroae* Rohwer, 1915, dorsal median carinae strongly elevated and extending at least 0.5 length of petiole (arrow).

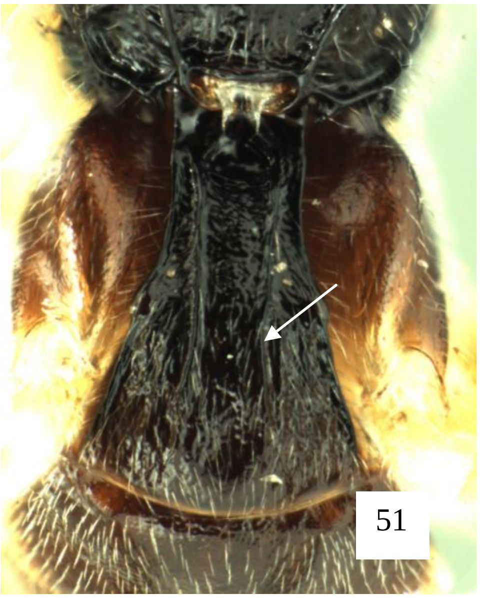


Fig. 52 Holotype *Polyblastus palustris* Habermehl, 1925, propodeum areolated.

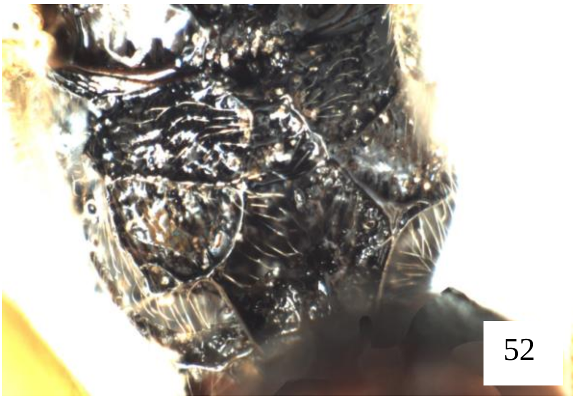


Fig. 53 Lectotype *Hodostatus brevis* Thomson, 1883, posterior field of propodeum sharply declivous in lateral view (arrow).

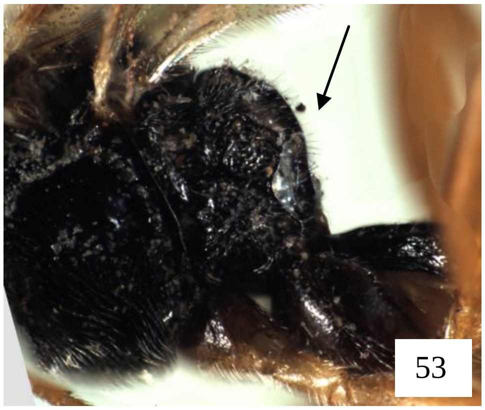


Fig. 54 *Polyblastus palustris* holotype, propodeal spiracle.

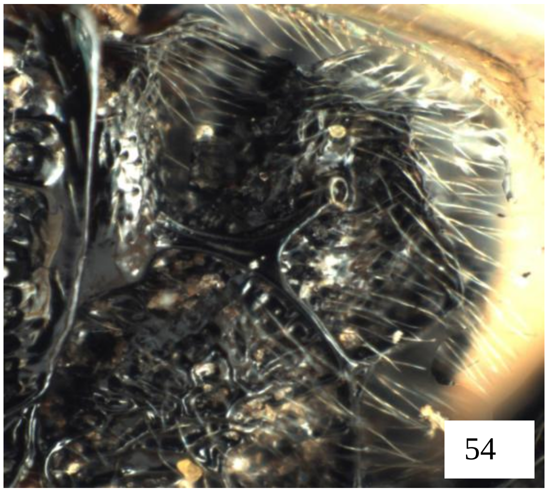


Fig. 55 Holotype *Polyblastus palustris* Habermehl, 1925 forewing showing a discrete but largely to almost entirely depigmented 3rs-m (arrow).

Fig. 56 Lectotype *Trematopygus rotundatus* Davis, 1897, propodeum and petiole densely granular-punctate to rugulose-punctate.

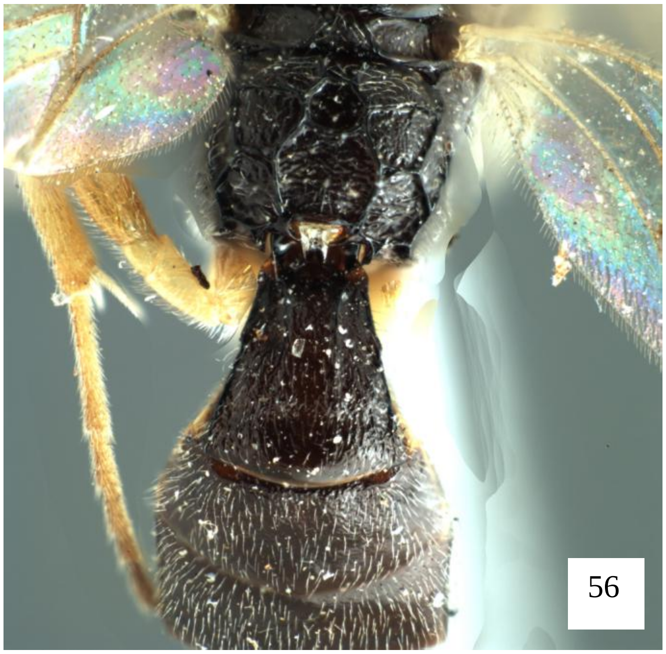


Fig. 57 Holotype *Hodostates schaffneri* Hinz, 1996, lateral habitus.

Fig. 58 *Hodostates schaffneri* male paratype, face sculpture finely granular matte.

Fig. 59 Holotype *Hodostates schaffneri* Hinz, 1996, lateral view, mesopleuron.

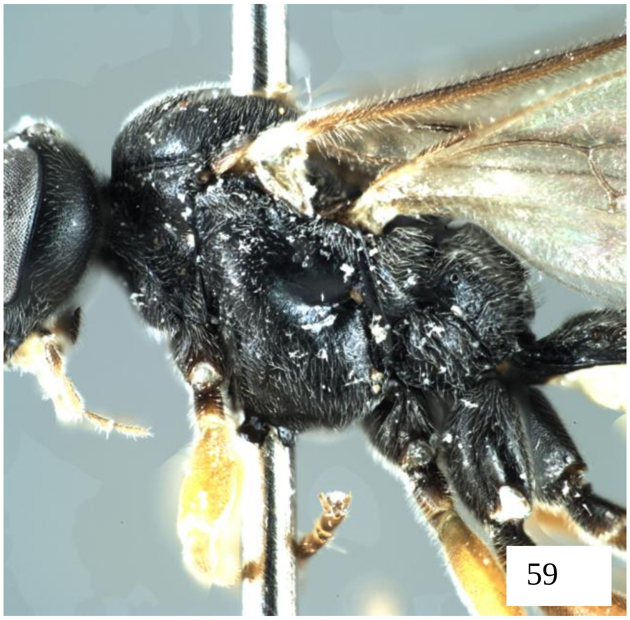


Fig. 60 *Hodostates schaffneri* male paratype, dorsal view, propodeum and petiole with dorsal median carinae strongly elevated medially (arrow).

Fig. 61 *Lethades* n. sp. holotype, right view, ovipositor (arrow) lacking a sub-apical dorsal notch.

Fig. 62 Nearctic species of *Lethades* Davis, 1897 with ovipositor lacking sub-apical dorsal notch.

APPENDIX B

TABLES

Table 1. Original designation and included subfamilies for informal groupings within Ichneumonidae.

	Pimpliformes	**Ichneumoniformes**	**Ophioniformes**
Original designation	Wahl (1990), Wahl and Gauld (1998)	Wahl (1993b)	Gauld (1985), Wahl (1991, 1993a)
Included subfamiles	Pimplinae, Rhyssinae, Diacritinae, Poemeniinae, Acaenitinae, Cylloceriinae, Orthocentrinae, Diplazontinae.	Ichneumoninae, Brachycyrtinae, Cryptinae.	Ophioninae, Campopleginae, Cremastinae, Tersilochinae, Banchinae, Ctenopelmatinae, Tatogastrinae, Anomaloninae.

Table 2. Species examined in subfamilies comprising the Ophioniformes

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**Angle A**	**Angle B**
Ophioninae species 1	0	3	1	0	1	1	-	-	1	1	1	0	2	1	1	0	0	1	0	1	1	0	0	59.96	66.31
Ophioninae species 2	0	2	0	0	1	3	-	-	1	1	1	0	2	1	1	0	0	1	0	1	1	2/1	2	81.89	71.69
Campopleginae species 1	1	3	0	0	1	3	0	0	-	1	2	0	0	1	1	0	0	0	0	1	1	2	2	45	45
Campopleginae species 2	1	1	2	0	1	3	-	-	1	1	2	0	0	1	1	0	0	0	0	1	1	1/2	3	46.44	1
Cremastinae species 1	2	0	0	0	1	3	-	-	1	1	1	0	0	1	1	1	0	1	0	1	1	1	3	45.17	1
Cremastinae species 2	1	0	0	0	1	3	-	-	1	1	1	0	3	1	1	1	0	1	0	1	1	1	3	45.17	1
Tersilochinae species 1	1	0	1	0	1	2	-	-	1	1	1	0	3	1	1	0	0	1	0	1	0	1	3	63.23	1
Tersilochinae species 2	1	0	0	0	1	0	-	-	1	1	1	0	3	1	1	0	0	1	0	1	0	0	0	78.75	78.75
***Banchus* species 1**	1	1	0	0	1	1	-	-	1	1	2	0	0	1	1	1	0	0	0	1	1	1	1	26.51	26.77
***Banchus* species 2**	1	1	0	0	1	1	-	-	1	1	2	0	0	1	1	1	0	0	0	1	1	1	1		
Anomaloninae species 1	0	2	0	0	1	3	0	1	1	1	1	0	3	1	1	0	0	0	0	1	1	2/1	2/1	53.13	75.41
Anomaloninae species 2	0	2	0	0	1	3	-	-	1	1	1	0	3	1	1	0	0	0	0	1	1	2/1	2/1		
Ctenopelmatinae																									
Pionini																									
***Labrossyta* species 1**	0	2	1	0	1	3	0	1	1	1	1	0	0	1	1	0	0	1	0	1	1	2/1	0	77.61	56.44
***Pion* species 1**	1	1	-	0	1	-	-	-	1	-	-	-	-	-	0	-	-	-	0	-	-	-	-		
***Sympherta* species 1**	0	2	-	0	1	-	0	0	1	1	2	-	2	0	0	-	-	-	0	-	-	-	-		
***Rhorus* species 1**	0	2	-	0	1	-	1	1	1	1	2	-	0	1	0	-	-	-	0	-	-	-	-		
***Treamtopygus* species 1**	0	1	-	0	1	-	0	0	1	1	2	-	3	0	0	-	-	-	0	-	-	-	-		
***Hodostates* species 1**	-	-	-	0	-	-	-	-	-	-	-	-	-	-	1	-	-	-	0	-	-	-	-		

Table 2. Continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Angle A	Angle B
***Lethades* species 1**	-	-	-	0	-	-	-	-	-	-	-	-	-	-	0	-	-	-	0	-	-	-	-		
Perilissini																									
***Absyrtus* species 1**	1/2	1/3	2	0	1	0/2	0	0	1	1	2	0	3/2	1	1	0	0	1	0	1	1	0	0	71.08/71.81	46.05/63.58
***Aechmeta* species 1**	1	1	0	0	1	0	0	0	1	1	2	0	-	1	1	0	0	1	-	1	1	2/1	2/0	69.79	63.19
***Lathrolestes* species 1**	1	3	2	0	1	0	0	0	1	1	2	0	2	1	1	0	0	0	0	1	1	0	0	71.81	79.52
***Lathrolestes* species 2**	1	2	1	0	1	2	0	0	1	1	2	0	-	1	1	0	0	0	0	-	0	0	0	84.88	85.26
Oetophorus pleuralis	1/2	1/2	2	0	1	3/2	0	0	1	0/1	0/2	0	0/2/3	1	1	0	0	1/0	0	1	1	0, 2/0 or 2/1	0 or 2/0	72.55/72.36/72.52/68.05	71.69/53.13/68.29 (2)
***Trematopygodes* species 1**	1/2	1	1	0	1	2	-	-	1	1	2	0	2	1	1	0	0	0	0	1	1	-	0	65.39	74.78
***Trematopygodes* species 2**	1	2	1	0	1	3	0	0	1	1	2	0	2	1	1	0	0	0	0	1	1	2/0	2/0	68.75	81.54
***Perilissus* species 1**	1	1	2	0	1	0	0	0	1	1	2	0	-	1	1	1	0	0	0	1	1	2/0	0	75.75	56.20
Mesoleiini																									
***Alexeter* species 1**	1	3	1	0	-	-	-	-	1	-	-	-	2	1	1	1	0	1	0	1	1	1	0	66.44	55.47
***Alexeter* species 2**	1	3	0	0	1	2	1	1	1	1	1	0	0	1	1	1	0	1	0	1	1	0	0	65.28	44.97
***Anoncus* species 1**	0	1	1	0	1	-	0	1	1	1	1	-	3	0	0	0	-	-	0	-	-	-	-		
***Barytarbes* species 1**	1	3	0	0	1	2	-	-	1	1	1	0	2	1	1	0	0	1	0	1	1	0	0	62.21	74.55
***Campodorus* species 1**	1	2	1	0	1	-	-	-	1	-	-	-	2	1	1	1	0	1	0	1	1	1	0	48.21	53.13
***Campodorus* species 2**	1	3	1	0	1	2	1	1	1	1	1	0	2	1	1	1	0	1	0	1	1	0	0	60.03	33.75

Table 2. Continued

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**Angle A**	**Angle B**
***Campodorus* species 2 (possible)**	1	3	0/1	0	1	3/2	1	1	1	1	1	0	2	1	1	0	0	1	0	1	1	0	0	71.81/67.09	59.13/60.18
***Campodorus* species 3**	1	2	1/0	0	1	2	1	1	1	1/0	1/0	0	2/0	1	1	1	0	1/0	0	1	1	0, 2/0	0	68.72/68.58/67.97/68.72	63.23/47.58/63.23/66.44
***Campodorus* species 4**	1	2	0	0	1	2	-	-	1	-	-	-	-	1	1	1	0	1	0	1	1	2/0	0	71.81	39.87
Mesoleiini species 1	1	3	1	0	1	2	-	-	1	1	1	0	2	1	1	0	0	1	0	1	1	2/0	0	65.23/57.94	45.04/45.17
Mesoleiini species 2	1	3	0	0	1	0	-	-	1	-	-	-	2	1	1	1	0	1	0	1	1	0	0	60.03	46.49
Mesoleiini species 3	1	3	0	0	1	-	-	-	1	-	-	-	-	1	1	1	0	1	0	1	1	1	0		
Mesoleiini species 4	1	2	0	0	1	2	1	1	1	1	1	0	0	1	1	0	0	1	0	1	1	2/0	0	72.83	47.58
Euryproctini																									
Euryproctini species 1	1	3	0	0	1	2	0	0	1	1	2	0	2	1	1	0	0	0	0	1	1	0	0	72.10	63.23
Euryproctini species 2	1	3	0	0	1	2	0	1	1	1	2	0	-	1	1	1	0	0	0	1	1	0	1	74.12	63.23
Euryproctini species 3	1	2	2	0	1	0	-	-	1	-	-	-	0	1	1	0	0	1	0	1	1	2/1	3	65.20	1
Euryproctini species 4	1	2	-	0	1	0	1	0	1	-	-	-	2	1	1	0	0	1	0	1	1	2/0	3	69.52/73.31	1

Table 3: Character states common to Ctenopelmatinae

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Angle A	Angle B
Pionini																									
***Labrossyta* species 1**	0	2	1	0	1	3	0	1	1	1	1	0	0	1	1	0	0	1	0	1	1	2/1	0	77.61	56.44
***Pion* species 1**	1	1	-	0	1	-	-	-	1	-	-	-	-	-	0	-	-	-	0	-	-	-	-		
***Sympherta* species 1**	0	2	-	0	1	-	0	0	1	1	2	-	2	0	0	-	-	-	0	-	-	-	-		
***Rhorus* species 1**	0	2	-	0	1	-	1	1	1	1	2	-	0	1	0	-	-	-	0	-	-	-	-		
***Treamtopygus* species 1**	0	1	-	0	1	-	0	0	1	1	2	-	3	0	0	-	-	-	0	-	-	-	-		
***Hodostates* species 1**	-	-	-	0	-	-	-	-	-	-	-	-	-	-	1	-	-	-	0	-	-	-	-		
***Lethades* species 1**	-	-	-	0	-	-	-	-	-	-	-	-	-	-	0	-	-	-	0	-	-	-	-		
Perilissini																									
***Absyrtus* species 1**	1/2	1/3	2	0	1	0/2	0	0	1	1	2	0	3/2	1	1	0	0	1	0	1	1	0	0	71.08/71.81	46.05/63.58
***Aechmeta* species 1**	1	1	0	0	1	0	0	0	1	1	2	0	-	1	1	0	0	1	-	1	1	2/1	2/0	69.79	63.19
***Lathrolestes* species 1**	1	3	2	0	1	0	0	0	1	1	2	0	2	1	1	0	0	0	0	1	1	0	0	71.81	79.52
***Lathrolestes* species 2**	1	2	1	0	1	2	0	0	1	1	2	0	-	1	1	0	0	0	0	-	0	0	0	84.88	85.26
Oetophorus pleuralis	1/2	1/2	2	0	1	3/2	0	0	1	0/1	0/2	0	0/2/3	1	1	0	0	1/0	0	1	1	0, 2/0 or 2/1	0 or 2/0	72.55/72.36/72.52/68.05	71.69/53.13/68.29 (2)
***Trematopygodes* species 1**	1/2	1	1	0	1	2	-	-	1	1	2	0	2	1	1	0	0	0	0	1	1	-	0	65.39	74.78
***Trematopygodes* species 2**	1	2	1	0	1	3	0	0	1	1	2	0	2	1	1	0	0	0	0	1	1	2/0	2/0	68.75	81.54
***Perilissus* species 1**	1	1	2	0	1	0	0	0	1	1	2	0	-	1	1	1	0	0	0	1	1	2/0	0	75.75	56.20

Table 3: Continued

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**Angle A**	**Angle B**
Mesoleiini																									
***Alexeter* species 1**	1	3	1	0	-	-	-	-	1	-	-	-	2	1	1	1	0	1	0	1	1	1	0	66.44	55.47
***Alexeter* species 2**	1	3	0	0	1	2	1	1	1	1	1	0	0	1	1	1	0	1	0	1	1	0	0	65.28	44.97
***Anoncus* species 1**	0	1	1	0	1	-	0	1	1	1	1	-	3	0	0	0	-	-	0	-	-	-	-		
***Barytarbes* species 1**	1	3	0	0	1	2	-	-	1	1	1	0	2	1	1	0	0	1	0	1	1	0	0	62.21	74.55
***Campodorus* species 1**	1	2	1	0	1	-	-	-	1	-	-	-	2	1	1	1	0	1	0	1	1	1	0	48.21	53.13
***Campodorus* species 2**	1	3	1	0	1	2	1	1	1	1	1	0	2	1	1	1	0	1	0	1	1	0	0	60.03	33.75
***Campodorus* species 2 (possible)**	1	3	0/1	0	1	3/2	1	1	1	1	1	0	2	1	1	0	0	1	0	1	1	0	0	71.81/67.09	59.13/60.18
***Campodorus* species 3**	1	2	1/0	0	1	2	1	1	1	1/0	1/0	0	2/0	1	1	1	0	1/0	0	1	1	0, 2/0	0	68.72/68.58/67.97/ 68.72	63.23/47.58/63.23/66.44
***Campodorus* species 4**	1	2	0	0	1	2	-	-	1	-	-	-	-	1	1	1	0	1	0	1	1	2/0	0	71.81	39.87
Mesoleiini species 1	1	3	1	0	1	2	-	-	1	1	1	0	2	1	1	0	0	1	0	1	1	2/0	0	65.23/57.94	45.04/45.17
Mesoleiini species 2	1	3	0	0	1	0	-	-	1	-	-	-	2	1	1	1	0	1	0	1	1	0	0	60.03	46.49
Mesoleiini species 3	1	3	0	0	1	-	-	-	1	-	-	-	-	1	1	1	0	1	0	1	1	1	0		
Mesoleiini species 4	1	2	0	0	1	2	1	1	1	1	1	0	0	1	1	0	0	1	0	1	1	2/0	0	72.83	47.58
Euryproctini																									
Euryproctini species 1	1	3	0	0	1	2	0	0	1	1	2	0	2	1	1	0	0	0	0	1	1	0	0	72.10	63.23
Euryproctini species 2	1	3	0	0	1	2	0	1	1	1	2	0	-	1	1	1	0	0	0	1	1	0	1	74.12	63.23
Euryproctini species 3	1	2	2	0	1	0	-	-	1	-	-	-	0	1	1	0	0	1	0	1	1	2/1	3	65.20	1
Euryproctini species 4	1	2	-	0	1	0	1	0	1	-	-	-	2	1	1	0	0	1	0	1	1	2/0	3	69.52/73.31	1

Table 4: Species of Pimpliformes, representeded by Diplazontinae, and other non-ophioniform subfamilies.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**Angle A**	**Angle B**
Pimpliformes																									
Pimplinae species 1	0	0	-	0	1	2	-	-	1	1	1	-	0	1	0	-	-	-	0	-	-	-	-		
Pimplinae species 2	0	0	-	0	1	2	-	-	1	1	2	-	0	1	0	-	-	-	0	-	-	-	-		
Orthocentrinae species 1	0	1	-	0	1	-	-	-	1	1	2	-	2	0	0	-	-	-	0	-	-	-	-		
Diplazontinae species 1	1	2/3	2	0	1	2	1	0	1	1	3	1	1	1	1	1	0	0	0/1	1	1	2/0	3	67.38/70.48	1
Diplazontinae species 2	1	3	2	0	1	3	-	-	1	1	1/2	1	3/1	1	1	0	0	0	0/1	1/0	1	0	0	62.50/59.96	57.68/63.23
Diplazontinae species 3	1	3	2	0	1	-	-	-	1	1	1	-	3	1	1	1	0	0	0	1	1	0	0	68.96	38.68
Diplazontinae species 4	1	3	2	0	1	2	1	0	1	1	2	1	1	-	1	0	0	0	0	1	1	0	0		
Diplazontinae species 5	1	1/2	0	0	1	2	-	-	1	-	-	-	1	0	1	0	0	0	0	1	1	2/1	1	78.75	29.04
Diplazontinae species 6	1	3	2	0	1	3	-	-	1	1	2/3	1	3	1	1	0	0	0	1	1	1	2/0	1	66.49/65.51	47.79
Diplazontinae species 7	1	2	2	0	2	-	-	-	1	-	-	-	1	1	1	0	0	0	0	1	1	2	1	67.55	11.31
Diplazontinae species 8	1	3	2	0	2	3	-	-	1	1	3	1	1	1	1	0	0	0	1	1	1	2/0	1	66.44	69.52
Diplazontinae species 9	1	3	2	0	1	-	-	-	1	1	2	1	1	1	1	1	0	0	1	1/0	1	0	1	56.21	56.81
Diplazontinae species 10	1	2	2	0	1	1	-	-	1	1	3	1	3	1	1	0	0	0	1	1	1	2/0	2/0	66.93	61.93
Ichneumoniformes																									
Ichneumoninae species 1	1	0	-	0	1	-	-	-	1	1	2	-	0	1	0	-	-	-	1	-	-	-	-		
Ichneumoninae speces 2	1	0	-	0	1	-	-	-	1	1	2	-	0	1	0	-	-	-	1	-	-	-	-		

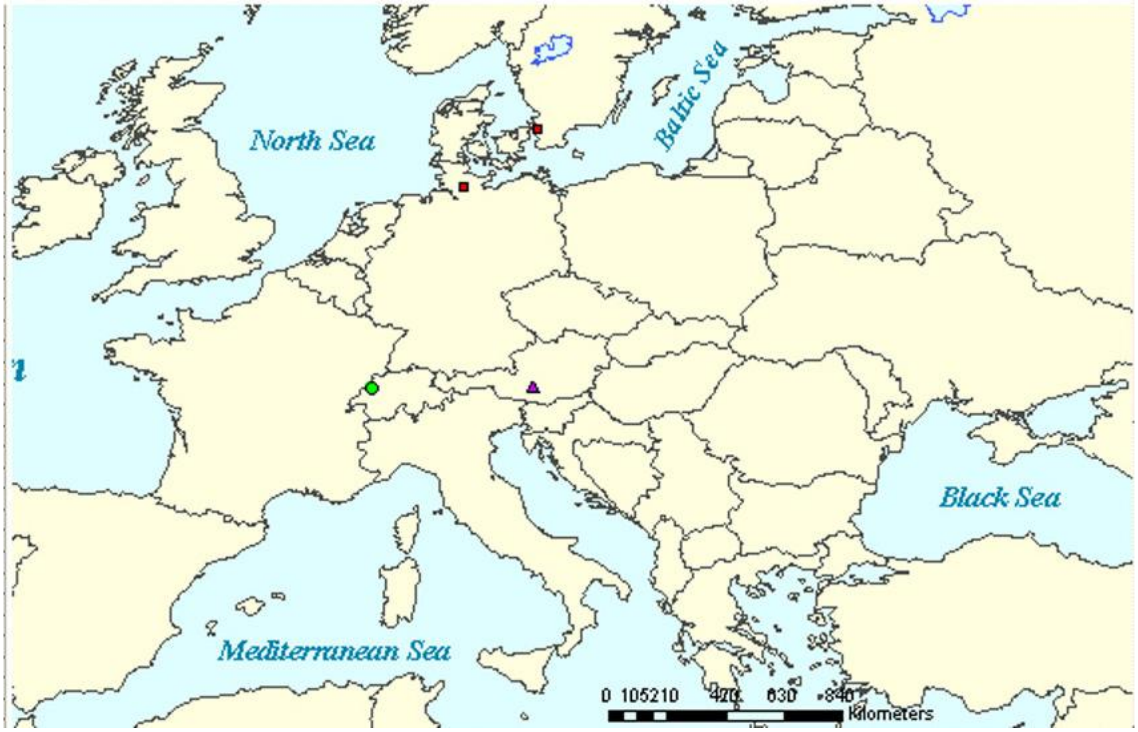
Table 4. Continued

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**Angle A**	**Angle B**
Cryptinae species 1	0	0	-	0	1	2	-	-	1	1	2	-	0	1	0	-	-	-	1	-	-	-	-		
Cryptinae species 2	0	0	-	0	1	2	-	-	1	1	2	-	0	1	0	-	-	-	1	-	-	-	-		
Mesochorinae species 1	0	2	-	0	1	-	-	-	1	1	1	-	3	1	0	-	-	-	-	-	-	-	-		
Mesochorinae species 2	0	2	-	0	1	-	-	-	1	0	-	-	3	1	-	-	-	-	-	-	-	-	-		
Metopius (Cultrarius) comptus	1	2	0	0	1	2	0	0	1	1	1	1	3	1	1	1	0	0	0	1	1	2/0	2/0	45.17	63.23
Exochus species 1	1	2	-	0	1	3	0	0	1	1	1	0	2	1	0	-	-	-	0	-	-	-	-		
Trieces species 1	1	2	2	0	1	3	0	0	1	1	1	0	2	1	1	0	0	0	0	1	1	2/0	1	80.70	56.44
Netelia species 1	0	1	-	0	1	-	-	-	1	1	2	-	3	1	0	-	-	-	0	-	-	-	-		
Tryphoninae species 2	0	1	-	0	1	-	-	-	1	1	2	-	3	1	0	-	-	-	0	-	-	-	-		
Xoridinae species1	0	0	-	1	1	-	-	-	1	0	-	-	0	1	0	-	-	-	0	-	-	-	-		
Xoridinae species 2	0	0	-	1	1	-	-	-	1	~1	1	-	0	1	0	-	-	-	0	-	-	-	-		
Labeninae	0	0	-	1	1	2	-	-	1	1	3	-	0	1	0	-	-	-	-	-	-	-	-		

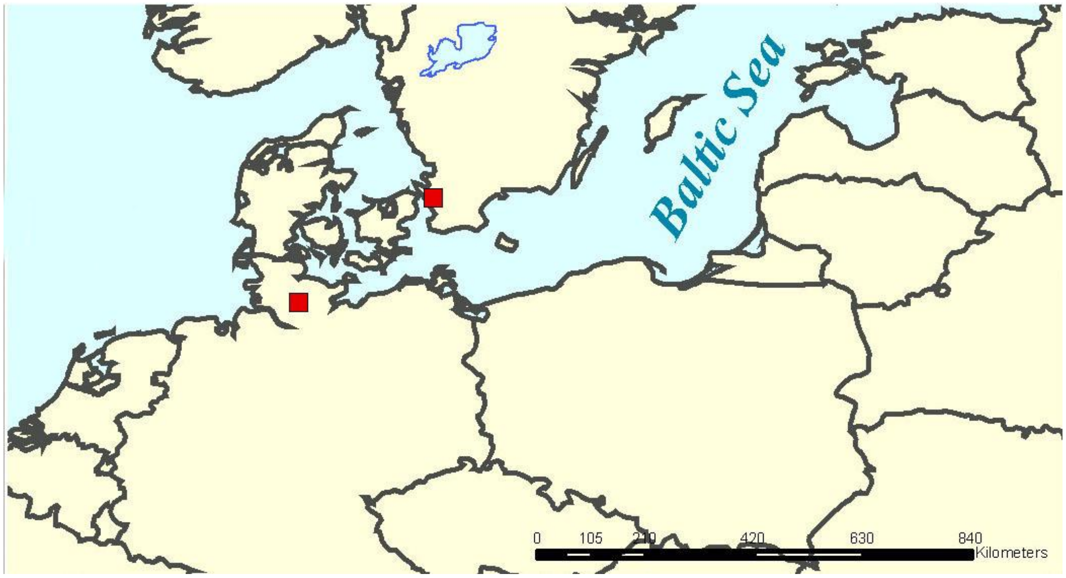
APPENDIX C

MAPS

Map 1. European distribution of *Hodostates brevis* (🟥), *Lethades schaffneri* (🟢), and *Lethades* sp. nov. (▲).

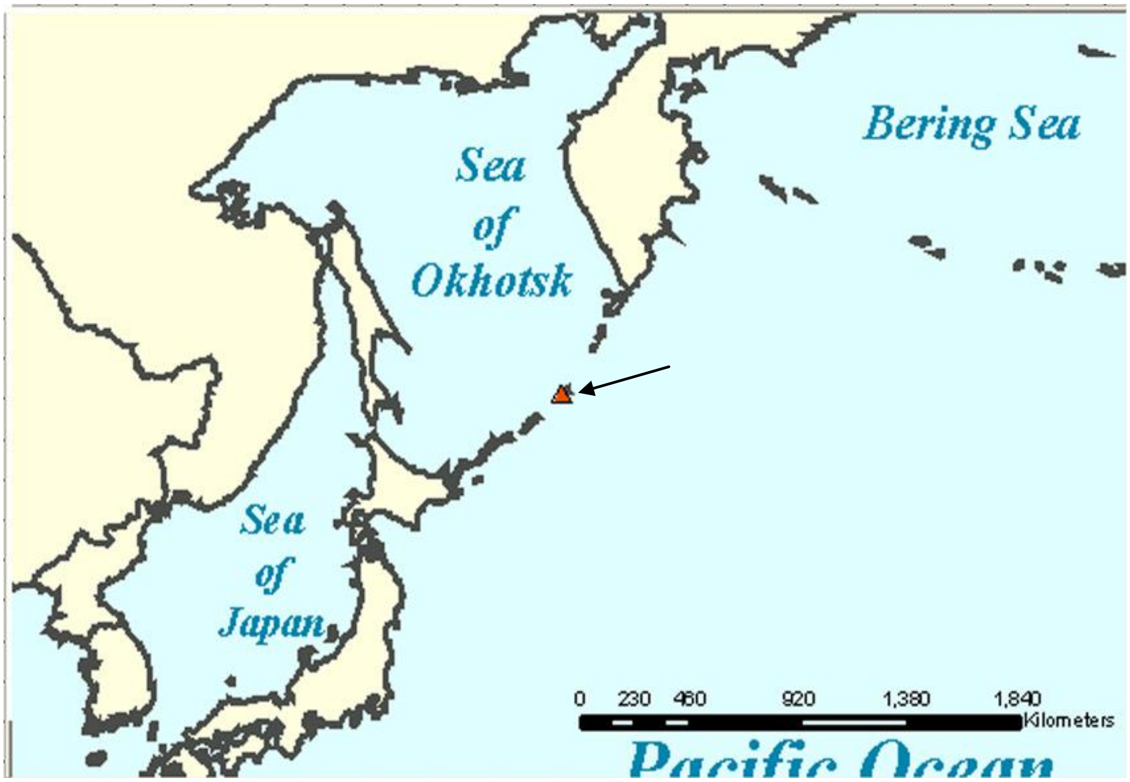


Map 2. European distribution of *Hodostates brevis*.



Map 3. Neartic distribution of *Hodostates rotundatus*.

Map 4 Distribution of *Hodostates kotenkoi* in Asia.



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