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Phylogenetic revision of the parasitoid wasp family Trigonalyidae (Hymenoptera)

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Abstract

A phylogenetic analysis of generic relationships and revised generic concepts for the Trigonalyidae are presented. The Trigonalyidae is divided into two subfamilies, the Orthogonalyinae and the Trigonalyinae. Orthogonalyinae consists of a single primitive genus, *Orthogonalys*, sharing many generalized apocritan characters, but lacking advanced trigonalyid characters including antennal tyloids and female metasomal armature. No synapomorphies have been detected for the Orthogonalyinae. Trigonalyinae are characterized by the presence of tyloids. The Trigonalyinae were originally defined by the absence of female armature, and were therefore polyphyletic because armature has been lost several times. Within the revised concept of Trigonalyinae, the tribe Trigonalyini is characterized by the presence of elongate parameres and an inter-torulus distance subequal to the distance between the torulus and the eye. A second tribe, Nomadinini, is based on the secondary loss of tyloids, and comprises the previous subfamilies Seminotinae, Nomadininae, Bareogonalinae, and Lycogastrinae. The two tribes Trigonalyini and Nomadinini share the presence of female armature, though in some Trigonalyini it has been secondarily lost. The genera *Labidogonalos* Schulz, *Lycogastroides* Strand, *Lycogonalos* Bischoff, *Nanogonalos* Schulz, *Poecilogonalos* Schulz and *Taiwanogonalos* Tsuneki are synonymized under *Taeniogonalos* Schulz. The species *Lycogaster zimmeri* Bischoff, *Tapinogonalos maschuna* Schulz, and *Trigonalys pictifrons* Smith (placed in *Lycogaster* by Schulz 1906) are transferred to *Taeniogonalos*. The genera *Discenea* Enderlein and *Stygnogonalos* Schulz are synonymized under *Trigonalys* Westwood. The species *Labidogonalos flavescens* Bischoff, *Labidogonalos sanctaecatharinae* Schulz, *Trigonalys lachrymosa* Westwood (placed in *Lycogaster* by Bischoff 1938), *Trigonalys maculifrons* Cameron (placed in *Labidogonalos* by Bischoff 1938), and *Trigonalys rufiventris* Magretti (placed in *Lycogaster* by Schulz 1907) are transferred to *Trigonalys*. *Trigonalys costalis* Cresson is sunk under *Taeniogonalos gundlachii* (Cresson). *Xanthogonalos fasciatus* Bertoni and *X. severini* Schulz are synonymized under *Trigonalys sanctaecatharinae* (Schulz). *Mimelogonalos partiglabra* Riek and *Mimelogonalos punctulata* Riek are synonymized with *Mimelogonalos bouvieri* Schulz. Lectotypes are designated for *Trigonalys melanoleuca* Westwood and *Taeniogonalos fasciatipennis* (Cameron). The author of *Trigonalys maculifrons* is Sharp 1895, not Cameron 1897, and the author of *Taeniogonalos enderleini* is De Santis 1980, not Schulz 1906. Viereck in 1914 designated *Trigonalys pulchella* Cresson as type of the genus *Tapinogonalos* Schulz, preceding Bischoff's 1938 designation, making *Tapinogonalos* a synonym of *Orthogonalys*. A new genus, *Afrigonalys*, is proposed for the three species that were described in "*Tapinogonalos*" *sensu* Bischoff, *nec* Viereck.

KEYWORDS: Trigonalyidae, phylogeny, Hymenoptera, parasitoid, hyperparasitoid, biogeography, homoplasy, convergence.

Introduction

Trigonalyids have a biology unique within the Hymenoptera. Thousands of eggs are laid on foliage (Figs 1-5) and these eggs will not hatch unless consumed by a herbivorous caterpillar or sawfly larva. The ultimate hosts of trigonalyids are the parasitoids or predators which attack the herbivore, although some species will directly parasitize sawflies. Some species of trigonalyids may parasitize hosts of different orders and sizes, resulting in a great deal of intraspecific variation and confusion. Weinstein & Austin (1991) recognized about 100 valid species and here we recognize xxx genera and xxx species, and have seen approximately xxx additional undescribed species. This group is rarely collected; and the hosts for most species, and many other aspects of the biology remains unknown. The biology of trigonalyids was reviewed in detail by Clausen (1940), Carmean (1991), and Weinstein & Austin (1991, 1995b). Chen (1949), Riek (1954, 1962a), Teranishi (1929), Townes (1956), Tsuneki (1991), and Smith (1996) are important regional references with keys, though they cover a limited number of taxa.

Most Trigonalyidae are relatively large (5-15 mm long), though some are as small as 3 mm. Some species are thin and elongate, mimicking ichneumonids (Fig. 6), while others are relatively stout-bodied, mimicking vespids (Figs 4-5). Superficial convergence among phylogenetically distant trigonalyids is common and appears to be due to unrelated species mimicking a common wasp model.

Schulz (1907a) undertook the only global study of trigonalyid generic relationships, and regional studies consistently mention the need for generic revision. Schulz probably had about 250 specimens available to him, about half of which were *Pseudogonalos hahnii* (Spinola), and most of his specific and generic descriptions were based on one or two specimens. As a result, his genera tended to be narrowly defined and based on variable characters. Bischoff (1933) remarked that under Schulz's system a new genus would be necessary for each new species. Benoit (1951) stressed the need for broadening generic concepts. Strand (1912) stated that Schulz had gone too far in his classification of genera and that his subfamilies were built on a weak foundation of variable characters. Weinstein & Austin (1991) noted "that many genera are poorly defined and that their monophyly, and that of some subfamilies, is questionable."

Since 1907 the numbers of Trigonalyidae collected, mainly through Malaise traps and rearing, has greatly increased. Because Schulz's genera were poorly defined and his generic keys confusing, different workers have placed species in unrelated genera, or have created new genera synonymous with existing ones. The purpose of this study is to revise generic concepts, to resolve some of the taxonomic confusion which resulted from a lack of understanding of the variability of genera and species, and to propose monophyletic higher taxa based on shared derived characters.

Monophyly and distinguishing characters of the Trigonalyidae

Despite the diversity of form within the family, the Trigonalyidae is clearly monophyletic, and is well-defined by a suite of derived morphological and behavioral characters. These characters clearly distinguish and separate the family from other groups, so that despite superficial mimicry there are no extant taxa that can be confused with Trigonalyidae. One feature unique to all members of the family is the presence of sparse white scales or setae on the outside of the middle flagellomeres of the female antenna (Fig. 13). At magnifications of X 30-50 they usually appear as an oval patch of sparse white spots. On dirty, wet, or greasy specimens they may not be visible. Additional features, apparently unique to trigonalyids but secondarily lost in *Nomadina* Westwood, *Bakeronymus* Rohwer, and *Pseudonomadina* Yamane & Kojima are: mandibles asymmetrical (Fig 19); hind trochantellus diagonally divided and appearing 2-segmented (=hind trochanters apparently 3-segmented); and propodeal spiracle covered by prominent flap. *Bareogonalos*, as well as *Nomadina*, *Bakeronymus*, and *Pseudonomadina*, always have the hind trochantellus undivided, and some species of *Bareogonalos* have symmetrical mandibles. Trigonalyids are also characterized by a supra-antennal elevation or raised area above and mesad of the torulus that may be reduced to absent in some _Bareogonalos_ and related genera (Figs 14-20). Other, possibly plesiomorphic, diagnostic characters are: maxillary palps longer than mandibles and 6-segmented, with first segment very small (maxillary palps as long as mandible and 4-segmented in _Bakeronymus_, rudimentary and 4 or fewer segments in _Nomadina_ and _Pseudonomadina_); tarsi with plantar lobes (Fig 21); tarsal claws cleft (Fig 21); forewing with pronounced costal cell and complete wing venation (generally 10 closed cells), hindwing with two closed cells; propodeal foramen open ventrally; and metasomal terga with short dorsolateral sutures (visible on tergum II and often covered on the following terga). Most trigonalyids have 18-28 antennal segments (16-26 flagellomeres), although some have as few as 13 segments and one specimen has been found with 32 segments. Tyloids (raised areas without pubescence)(Figs 10-12) on the outside of the middle antennal segments of males of many species are not part of the groundplan but are derived within the family. Females of many species have 'metasomal armature' (Figs 1-3), i.e., projections or raised ledges, posteriorly on sternum II or III or both, a feature also derived within the family and not part of the groundplan.

Distribution

Trigonalyidae have a cosmopolitan distribution, with the exception of arctic and alpine regions. The greatest abundance of taxa occur in the tropics and only one species is found in Europe. Most genera are widely distributed. For example, _Orthogonalys_ Schulz is known from Japan, Taiwan, northwestern Vietnam, northeastern India, Madagascar, Tanzania, eastern South America, and eastern North America. _Taeniogonalos_ Schulz is even more widespread, and is found in these areas as well as in Australia, Papua New Guinea, the Solomon Islands, Indonesia, Sri Lanka, and throughout India. Some genera are more restricted, e.g., _Mimelogonalos_ Schulz from Australia (with an undescribed close relative in Papua New Guinea) and _Seminota_ Spinola from the neotropics. _Nomadina_ is also known only from the neotropics, but there are two closely related Asian genera, _Bakeronymus_, with a single species known only from the Philippines and Taiwan, and _Pseudonomadina_, known only from the Philippines. _Bareogonalos_ is found around the perimeter of the Pacific Ocean, in western Mexico, northwestern North America, eastern Siberia, Japan, Taiwan, Java, and Sumatra. The same species of _Bareogonalos_ is found in Siberia, Japan, and Java. Other trigonalyid species found in Indonesia may be distributed as far away as India [_Taeniogonalos_ _thwaitesii_ (Westwood)] and China [_Lycogaster celebesiensis_ (Szepligeti) and _Taeniogonalos fasciata_ (Strand)].

Distributions of trigonalyid genera linking widely separated regions are supporting evidence for the ancient origins of the group and appear to be relictual. However, none of the known hosts, except for sawflies, can be considered ancient. The most widely distributed trigonalyid, _Taeniogonalos_, is a relatively derived genus known to directly parasitize sawflies as well as indirectly tachinids and ichneumonids (Weinstein & Austin, 1991). The least derived trigonalyid, _Orthogonalys_, is widely distributed, absent only from Europe and Australia. Host information for the genus is limited to a few rearings from Lepidoptera pupae which are believed to be intermediate hosts and a tachinid parasitoid of Lepidoptera (see generic discussion).

Systematics

What little systematic stability this family has enjoyed historically has been an artifact due to its obscurity and the difficulty in developing adequate generic concepts. Schulz (1907a) and those who followed him placed the most distinct and autapomorphic genera, e.g., _Bareogonalos_, _Seminota_ (with _Xanthogonalos_ Schulz), and _Nomadina_ (with _Bakeronymus_) in their own subfamilies. The remaining genera were either united in one subfamily (Bischoff, 1938), or divided into two subfamilies, based on the presence or absence of female metasomal armature (Schulz, 1907a; Benoit, 1951; Weinstein & Austin, 1991). Although the armature is an obvious character unique to the trigonalyids, it has been lost independently in some species of the genera _Taeniogonalos_ and _Trigonalys_. In addition, armature presence or absence varies geographically in the species _Taeniogonalos thwaitesii_, and Riek (1962a) used a series of figures to show that the armature of _Taeniogonalos venatoria_ Riek also varies from prominent to reduced. Therefore, it is clear that other characters, in addition to armature, must be considered in assigning species to subfamilies, tribes, and genera.

Previously, venational characters were given considerable weight in defining genera (Cameron, 1899) and subfamilies (Schulz, 1905). Some of these characters are now known to vary even between the left and right side of individual specimens. Indeed, Benoit (1951) argued against using the form and size of the submarginal cells as an important systematic character. However, if many specimens are available, some generalizations may be informative. For example, while there are exceptions, most _Orthogonalys_ have a petiolate submarginal cell II, as do most _Nomadina_ that we examined. _Mimelogonalos_, _Lycogaster_, and _Bareogonalos_ consistently have submarginal cell II broadly attached, while many _Taeniogonalos_ and _Trigonalys_ are intermediate, so that Rs meets 1m-cu, with enough variation so that the submarginal cell is sometimes petiolate or broadly attached.

Because the ultimate host is not selected at oviposition, the size of the host can vary considerably, and thus the size of individuals within a trigonalyid species can also vary greatly. The extent of markings can also vary. Tsuneki (1991) illustrated and discussed the range of variation possible in the size and markings of _Taeniogonalos sauteri_ Bischoff. Series of specimens collected at the same location and time often have individuals that depart from the norm for what is considered a definitive character. For example, a specimen of _Seminota marginata_ (Westwood) has symmetrical mandibles [BMNH] or one _Bareogonalos jezoensis_ (Uchida) has a flat dorsellum [CARM]. This variation and anomaly makes it difficult to establish valid differences among species, especially when few specimens are available.

Finally, most earlier workers incorrectly believed that the metasomal armature was found on males only (Banks, 1908; Buysson & Marshall, 1892; Cameron, 1897, 1899; Cresson, 1865; Harrington, 1898; Magretti, 1897; Schrottky, 1906; Smith, 1851; Westwood, 1841, 1843) and thus identified females with metasomal armature as males. Even Schulz (1905) initially made this error, although his later works were accurate.

Methods and Materials

Morphological terminology follows that of Gauld and Bolton (1988), except that the terms *mesosoma*, *metasoma*, *sternum*, and *tergum* are used here. The term metasomal *armature* is used for the various modifications (projections, stout spines, or raised posterior edges) found on sterna II and/or III of some females. The *awl* is the sclerotized tip of the terminal sternum of the female that is shaped and functions like a hypodermic needle to pierce foliage for the oviposition of eggs (Yamane & Yamane, 1975, Fig. 16). In many cases it is held in the preceding sterna which are flattened into a *capsule* (Figs 1-3). The term *supra-antennal elevation* (SAE) is used for any elevation or modification above and mesad of the torulus (Tsuneki, 1991). The number of antennal 'segments' includes the scape, pedicel, and flagellomeres. Malar space is "short" if it is shorter than the width of the first flagellomere, "long" if it is longer. Only the metasomal segments are used for counting sterna and terga. Forewing (FW) length is measured from the break between the costal vein and the humeral plate to the wing tip. Body length is measured from the antennal insertion to the furthest point of the metasoma, and is not standardized due to changes in alignment of the head and metasomal segments. To see the angle of the gena in the horizontal plane, the termination of the genal carina, and whether the genal carina is mesad of or on the genal angle the head must be oriented so that it is viewed ventrally (Figs 22, 23).

Clausen (1940), Cooper (1954), Carlson (1979), and Gelhaus (1987) used the term secondary host for the folivore while Gauld and Bolton (1988) and Weinstein & Austin (1991) used the term primary host. Because of this ambiguity, we use the terms *intermediate host* when a trigonalyid needs to develop to adulthood in a second host, and *ultimate host* for the host that the larva uses to complete its development.

While trigonalyids from key geographical regions, including Southeast Asia, Africa, and South and Central America remain undercollected, we have had about 2300 specimens from over 50 collections available for study. Most genera were represented by series of 40 or more specimens. Still, many species and some genera are represented by only one to a few specimens, often of one sex, and many other species originally described from one to a few specimens remain unknown to us. We have seen the types (holotypes, syntypes, or lectotypes) of 37 species, including eleven types previously listed as missing or with their deposition unknown (Weinstein & Austin, 1991). We have seen paratypes of an additional nine species. The types of many species are apparently lost (Weinstein & Austin, 1991), and the species descriptions are often inadequate to determine their identity.

The characters in the data matrix (Table 1) are identified by numbers assigned in the section on character analysis; these numbers serve to identify the characters in the cladograms (Figs 24-30). The terminal taxa used in the analyses are the hypothetical ancestor and the genera of Trigonalyidae. So that results from the phylogenetic analysis would challenge our generic definitions and synonomizations, we also included species representing the previously recognized (and here synonymized) genera *Labidogonalos*, *Nanogonalos*, and *Poecilogonalos* Schulz, as well as taxa whose placement is tentative, including *Taeniogonalos flavocincta* (Teranishi) and *Taeniogonalos maga* (Teranishi). Due to the small number of specimens and in some cases their poor condition, it may not be possible to evaluate the relationships of Tsuneki's new genera and species until more specimens are collected (Tsuneki, 1991).

Parsimony analyses were carried out using MacClade 3.01 (Maddison & Maddison, 1992) and PAUP 3.0s (Swofford, 1991). MacClade was used for entering data and comparing different phylogenetic hypotheses (cladograms) and character evolution while PAUP was used for finding the most parsimonious trees and their statistics. PAUP's default heuristic search settings were used with more than fourteen taxa, and 100 random stepwise-addition replicates were used to search for additional parsimonious trees. With fewer than fourteen taxa, we used the branch and bound search, which will find all the most parsimonious trees.

Hennig86 ver. 1.5 (Farris, 1988) was also used for parsimony analyses. Polymorphic characters in the data matrix (Table 1) were converted to monomorphic characters using the ACCTRAN option in MacClade on the tree in Fig. 28. In the case of the propodeal scutellum of _Xanthogonalos_ the polymorphism was not resolved, so the character state was changed to unknown, resulting in a tree one step shorter. This file was exported to Hennig86, and then analyzed using the implicit enumeration option, which will find all the most parsimonious trees, and successive approximations character weighting (Farris, 1969). The Hennig86 file was imported back to PAUP, and reanalyzed, giving the same results as the original PAUP input file with polymorphic characters.

In the species lists, no attempt is made to duplicate the catalogues of Bischoff (1938) and Weinstein & Austin (1991). Synonymies and bibliographic details listed by them are not repeated except for clarification. Type repository information is based on Weinstein & Austin (1991) and our correspondence with the collections. Repository and label information is given for specimens examined of less common species in Carmean (1993). In a few cases we transferred or synonymized species without seeing the types because the type species of the genus they were placed in (_Poecilogonalos_, _Nanogonalos_, and _Discenea_) was also transferred, or because, based on the description, they were obviously misplaced.

Collection Abbreviations

Specimens were obtained from the following collections and individuals, using standard abbreviations from Arnett _et al_. (1993) for institutions and the first four letters of the last name for personal collections: AEIC- American Entomological Institute, Gainesville, D. Wahl; AMNH- American Museum of Natural History, New York, E.L. Quinter; ANIC- Australian National Insect Collection, Canberra, I. Naumann; ANSP- The Academy of Natural Sciences of Philadelphia, D. Azuma; BMNH- Natural History Museum, London, L. Ficken, T. Huddleston, I. Gauld, and M.C. Day; BPBM- Bishop Museum, Honolulu, K. Arakaki; CARM- D. Carmean personal collection; CASC-

California Academy of Sciences, San Francisco, W.J. Pulawski; CDAE- California Department of Food and Agriculture, M. Wasbauer; CMNH- The Carnegie Museum of Natural History, J. Rawlins; CNCI- Canadian National Collection, Ottawa, L. Masner and J. Huber; CUIC- Cornell University, Ithaca, J.K. Liebherr; DENH- University of New Hampshire, D.S. Chandler; EMUS- Utah State University, T. Griswold and F.D. Parker; FSAG- Collections Zoologiques, Gembloux, J. Leclercq; FSCA- Florida State Collection of Arthropods, Gainesville, J. Wiley; HNHM- Hungarian National Museum of History, Budapest, J. Papp; IMLA- Fundacion Miquel Lillo, San Miguel de Tucuman, A. Willink; INBIO- Instituto Nacional de Biodiversidad, Costa Rica, D. Janzen; INHS- Illinois Natural History Survey, Champaign, K.C. McGiffen; ISNB- Institut Royal des Sciences Naturelles de Belgique, Brussels, P. Dessart; IZAV- Universidad Central de Venezuela, Maracay, Venezuela, J.L. Garcia R.; KIMS- L. Kimsey personal collection, Davis; LACM- Natural History Museum of Los Angeles County, Los Angeles, R.R. Snelling; LEMQ- Lyman Entomological Museum, McGill University, Quebec, P.M. Sanborne; LSUC- Louisiana State University, V. Mosely and C.B. Barr; MACN- Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, A. Bachmann; MAMU- Macleay Museum, Sydney, Australia, D.S. Horning, Jr.; MCZC- Harvard Museum of Comparative Zoology, Cambridge, Massachusetts, D. Furth; MEMU- Mississippi Entomological Museum, Mississippi State University, T.L. Schiefer; MLPA- Universidad Nacional de La Plata, Ricardo A. Ronderos; MNHN- Museum National d'Histoire Naturelle, Paris, J.C. Weulersse; MRAC- Musee Royal de l'Afrique Centrale, Tervuren, E. De Coninck; MRSN- Spinola Collection, Museo Regionale di Scienze Naturali, Torino; MZSP- Museu de Zoologia da Universidade de São Paulo, C.R.F. Brandão; NCSU- North Carolina State University, Raleigh, R.L. Blinn; NHMW- Naturhistorisches Museum, Vienna, M. Fisher; NHRS- Naturhistoriska Riksmuseet, Stockholm, B. Gustafsson; OMNH- Osaka Museum of Natural History; OSUO- Oregon State University, Corvallis, G. Ferguson and J.A. DiGiulio; OXUM- Oxford Museum (Hope Entomological Collections), Oxford, C. O'Toole; PAGL- G. Pagliano personal collection, Torino; PORT- C.C. Porter personal collection, Gainesville; PSUC- Frost Entomological Museum, Pennsylvania State University, D.W. Love; RMNH- Rijksmuseum van Naatuurlijke Historie, Leiden, C. van Achterberg; ROME- Royal Ontario Museum, Toronto, C. Darling; SCAR- L. Scaramozzino personal collection, Torino; TAMU- Texas A&M University, E.G. Riley; TARI, Taiwan Agricultural Research Institute, L.Y. Chou; TMSA- Transvaal Museum, Pretoria, K.N. Dower; UCDC- Bohart Museum of Entomology, University of California, Davis, S. Heydon; UCRC- University of California, Riverside, S. Frommer; UOPJ- University of Osaka, Hirowatari; UMMZ- University of Michigan, Ann Arbor, M. O'Brien and B.M. OConnor; USNM- United States National Museum, Washington D.C., D.R. Smith and G.F. Hevel; WSUC- Washington State University, Pullman, R.S. Zack; YAMA- Sk. Yamane personal collection, Kagoshima; ZMHB- Zoological Museum of Humboldt University, Berlin, F. Koch; ZMUC- Universitetets Zoologiske Museum, Copenhagen, B. Petersen; ZSMC- Zoologische Staatssammlung, Munich, E. Diller. Abbreviations for other institutions mentioned in the text are: EIHU- Hokkaido University, Sapporo; MCSN- Museo Civico di Storia Naturale, Genoa; MLUH- Universität Halle, Halle.

Outgroup analysis

Trigonalyidae have been placed in or near most other major lineages of apocritan hymenopterans at one time or another. Recently, Whitfield (1992), Rasnitsyn (1988), and Johnson (1988) placed the Trigonalyidae in the Evaniomorpha, along with the Evanioidea, Ceraphronoidea, and the Megalyridae. Rasnitsyn (1988) considered the Stephanidae also to be evaniomorphs but Whitfield (1992) placed the Stephanidae basal to all other Apocrita. Whitfield (1992) also considered a second possibility, with the Trigonalyidae part of an unresolved trichotomy between Trigonalyidae, Evaniomorpha, and the 'Microhymenoptera'. Dowton and Austin (1994), using DNA sequence from the mitochondrial 16S rRNA gene, found the Trigonalyidae close to the base of the Apocrita along with the Evanioidea, but otherwise unresolved. Basibuyuk & Quicke (1995) found the structure of the basitarsal comb in the Trigonalyidae and Evaniidae, but not other proposed Evaniomorpha, to be almost identical. Like the other families in the Evaniomorpha, trigonalyids have the derived character of an elongated mesal lobe on the surface of the mesocoxa (Johnson, 1988).

The Trigonalyidae are so divergent morphologically from all the other Hymenoptera that outgroup analysis for most characters is speculative. Of the 30 characters used in this study, 23 can be found in the outgroups and contribute to outgroup analysis, including 2 of the 20 morphological characters that Shaw (1990) used in his analysis of the Megalyridae. The ancestral states of these later two characters are areolate-rugose propodeal sculpturing and elongate flagellomeres. Elongate body-form is the ancestral state for megalyrids (Shaw, 1990) and appears ancestral in trigonalyids, but because of intermediate states was not used in our analysis. Comparing trigonalyids with other Evaniomorpha, the Ceraphronoidea have metasomal tergum I longer than all the following terga, the antennae close to the mandibles, reduced wing venation, a long malar space, and the genal carina meeting the hypostomal carina. The Evaniidae have a long malar space, with the genal carina just mesad of the relatively sharp genal angle, and ending at the mandibular base.

Aulacidae have a long malar space, genal carina usually meeting the hypostomal carina (in some taxa ending at the mandibular base instead), and a propodeal foramen that is evenly curved or 'U'-shaped dorsally. Stephanidae have a long malar space, genal carina ending near the hypostomal carina, and a 'U'-shaped propodeal foramen (which is otherwise very different from the form in Trigonalyidae). No trigonalyids have reduced wing venation or an elongate first metasomal segment. In addition, trigonalyids have the antenna far removed from the mandible, except the derived *Pseudonomadina* and *Bakeronymus*. We conclude that the ancestral trigonalyid, as in most evaniomorphs, had the genal carina ending near the hypostomal carina, a 'U'-shaped propodeal foramen, and a long malar space, although this feature is too ambiguous in most taxa to be included in the analysis. The ancestor probably lacked such advanced trigonalyid characters as male tyloids, female armature, and sclerotization in the last female abdominal sternum.

We used two outgroups separately: one is based on the presumed primitive Evaniomorpha and is here called the *Evaniomorph* while the other is based on the hypothetical ancestral trigonalyid groundplan and is called the *Ancestor*. The Evaniomorph is based on the families Stephanidae, Aulacidae, Evaniidae, Gasteruptiidae, and Megalyridae. Characters for Megalyridae were taken from the literature (Naumann, 1991; Shaw, 1990). The Ancestor is similar but is influenced by *Orthogonalys* and has the family synapomorphies of asymmetrical mandibles and trochantellus divided; the character state for the SAE is unknown in the ancestor while in the evaniomorph outgroup it is flattened. The number of antennal segments is greater than 17 in the ancestral trigonalyid and less than 17 in the evaniomorph. The shape of the propodeal foramen is a low 'U' shape in the ancestor and unknown in the evaniomorph. The remaining characters have the same state in the ancestor and the evaniomorph. The ancestor and the outgroup were used separately in the parsimony analyses, and the exact same results were obtained from each, with *Orthogonalys* basal to the rest of the Trigonalyidae (Fig. 24).

Character Analysis

Characteristics used in this analysis are discussed below. Their inferred primitive and derived states are discussed below and in the previous section on outgroup analysis. When the evaniomorph or ancestral outgroup state could not be deduced, it has been coded as unknown (?) because it contributes no information about polarity of character state change. Characters were treated as unordered and reversible, and not weighted except in one analysis using *a posteriori* successive approximation character weighting (Farris, 1969). Inferences about polarity, based upon outgroup comparison, are given below; but ultimately polarity was determined after the cladistic analysis as a consequence of outgroup rooting of the trees. The data matrix is presented in Table 1.

1. *Head shape*. (0) Rounded, normal (Figs 14-17; Tsuneki, 1991 Figs 49, 156); (1) subrectangular and wide (in anterior view) (Figs 18, 20; Yamane & Yamane, 1975 Fig. 5; Yamane & Kojima 1982 Figs 1a, 2a; Tsuneki, 1991 Figs 2, 29). Heads of evaniomorphs are generally rounded and tall. *Bareogonalos*, *Nomadina*, *Pseudonomadina*, and *Bakeronymus* have the derived state.
2. *Vertex shape*. (0) Normal, convex, or flat (Figs 14-18, 20); (1) concave. Only two Asian genera, *Bakeronymus* and *Pseudonomadina*, have their head deeply indented along the dorsal sagittal plane, and this is apparently the derived condition.
3. *Supra-antennal elevation* (SAE). (1) Prominent, meeting or nearly meeting at midline (Fig. 14); (2) prominent, not meeting at midline; (3) reduced to small triangular protuberance and extending toward midline (Fig. 17); (4) flattened, not extending toward midline, flat between toruli (Figs 15, 18). This character was used extensively by Schulz (1907a) and Tsuneki (1991). In all other evaniomorphs there is no SAE: the area above and mesad of the torulus is flat, or the torulus is on a shelf. The ancestral condition is unknown, and the evaniomorph outgroup is coded as SAE flattened with the area between the toruli flat. In *Orthogonalys* the

SAE is generally prominent, projecting forward, and slightly separated at the midline. In *Taeniogonalos* the SAE is reduced so that the dorsal edge of the torulus forms a small triangular lip, and the intertorulus area is relatively flattened. In the Nomadinini the SAE is reduced and the intertorulus area is generally very flattened.

4. *Intertorulus Distance*. (0) Short, distance between toruli less than 0.9 times the shortest distance between the inner eye margin and the torulus; (1) medium, the two distances about equal; (2) long, toruli set far apart, shortest distance between inner margins of the toruli greater than the shortest distance between the inner eye margin and the outer edge of the torulus. In most evaniomorphs, and *Orthogonalys*, the intertorulus distance is short; this is assumed to be the ancestral condition. The distance is long in the Stephanidae.
5. *Toruli placement*. (0) Distant from mandibular base; (1) next to mandibular base. The toruli are above the clypeus, far removed from the mandibular base in most evaniomorphs and in most Trigonalyidae. The derived condition is only found in *Bakeronymus* and *Pseudonomadina*.
6. *Number of antennal segments*. (0) Greater than 17 segments (including scape and pedicel in count); (1) 13-16 segments. There is a great amount of variability in antennal segment number but no overlap between these states. Most Trigonalyidae have greater than 17 segments and this is considered the ancestral condition. Only *Nomadina*, *Bakeronymus*, and *Pseudonomadina* have 13-16 antennal segments and, as they are otherwise relatively derived genera, this is assumed to be the derived condition. However, the evaniomorph outgroup taxon is coded as having 13-16 segments since most evaniomorphs, except the Stephanidae, have their antennae with 13-14 segments or less.
7. *Antennal shape*. (0) Filiform; (1) thickened or spindleform. The evaniomorphs and most Trigonalyidae have filiform antennae of even thickness, though the Stephanidae have much thinner flagellomeres. The derived state occurs in

Seminota, *Lycogaster*, *Nomadina*, and related genera. A single undescribed male from Costa Rica with tyloids has spindleform antennae (AEIC), but in other respects it is close to *Taeniogonalos*, and its antennal shape is considered convergent.

8. *Tyloids*. (0) Absent; (1) present. Tyloids (Figs 10-12) are not present in the evaniomorphs or *Orthogonalys* and their presence is considered derived.

9. *Tyloid shape*. (1) Short, oval-round (Fig. 11); (2) elongate-broadly oval (Fig. 12); (3) elongate-narrow (Fig. 10). The shape of the tyloids has been generally ignored by previous authors but is valuable phylogenetically. The states are not ordered. To avoid giving additional weight to the absence of tyloids, this character is coded as unknown for taxa that lack tyloids, including the ancestor. We separated the character of tyloid presence from tyloid shape because we believe that change between different shapes is a different process than the gain or loss of tyloids. However, the topology of the strict and majority rule consensus trees was unchanged when these characters were combined (at the same time characters 27 and 28 were similarly combined) and when the ancestral state was 'tyloids absent', and the three tyloid shapes were treated as unordered and derived.

10. *Genal carina*. (0) Meets (or ends near) hypostomal carina (Fig. 9; Tsuneki, 1991, Fig. 64); (1) meets (or ends near) lateral edge of mandibular base (Figs 22, 23). The primitive state occurs in *Orthogonalys* and most evaniomorphs.

11. *Occiput excavation*. (0) Occiput not excavated (Fig. 9; Tsuneki, 1991, Fig. 64); (1) occiput slightly excavated (Fig. 23); (2) occiput deeply excavated but not near mandible; (3) occiput deeply excavated all the way to mandible (Fig. 22). In the ancestral condition, shared by *Orthogonalys* and the evaniomorphs, the genal carina is on a flat plane, and the occiput is not excavated. In *Pseudogonalos* the occiput is deeply excavated, but this ends in a flat plane before the mandible. The occiput of *Trigonalys* is deeply excavated all the way to the mandible. In *Taeniogonalos* the occiput is only slightly excavated.

12. *Genal angle*. (0) Located laterad of genal carina; (1) at genal carina. In most Trigonalyidae and evaniomorphs the genal angle is located laterad of the genal carina (Figs 9, 23). The genal angle and genal carina only overlap in *Trigonalys* (Fig. 22); this is the derived state.

13. *Clypeal width*. (0) Wider than base of antennae; (1) as wide as base of antennae. The derived state is only found in the most specialized of Trigonalyidae: *Nomadina*, *Bakeronymus*, and *Pseudonomadina*. In the ancestral condition and the normal apocritan condition, the clypeus is wider than the distance between the base of the antennae.

14. *Mandible symmetry*. (0) Asymmetrical; (1) symmetrical. In most Trigonalyidae there are three teeth on the left mandible and four on the right mandible (Fig. 19), rarely, there are four on the left and five on the right. The normal apocritan condition is symmetrical, and in several taxa within the Nomadinini the mandibular teeth are symmetrical. No other hymenopteran families are known to have asymmetrical mandibles as their groundplan. The groundplan synapomorphy for the family is believed to be asymmetrical and the evaniomorph outgroup condition is symmetrical.

15. *Maxillary palps*. (0) Normal, 6-segmented, as long or longer than mandibles; (1) 4-segmented, shortened or rudimentary. In most taxa the palps are much longer than the mandibles and this is considered the ancestral condition for Trigonalyidae. In *Bakeronymus*, *Nomadina* and *Pseudonomadina* the palps are usually 4-segmented, but in the latter two genera they are rudimentary and may be indistinctly segmented.

16. *Notauli of mesoscutum*. (0) Straight; (1) parallel at base and then diverging strongly. Only *Bakeronymus* and *Pseudonomadina* have curved notauli, making the median mesoscutal area nearly heart-shaped (Yamane & Kojima, 1982, Fig. 9). The evaniomorphs and most trigonalyids have relatively straight notauli.

17. *Submarginal cell II*. (1) Petiolate; (2) not petiolate. This character has been overemphasized in the past, and is somewhat variable within genera, but it is still phylogenetically informative. In most evaniomorphs venation is not comparable, except in the Aulacidae where the submarginal cell II is petiolate. Thus the ancestral and outgroup states are unknown. In *Trigonalys* and *Taeniogonalos* this character is variable, and was coded as unknown.

18. *Hind trochantellus*. (0) Divided; (1) undivided. Most Trigonalyidae have the trochantellus diagonally divided into two apparent segments and this is believed to be the ancestral condition for the Trigonalyidae. The evaniomorph outgroup was coded as undivided because they have the trochantellus undivided as do the derived genera *Bareogonalos*, *Nomadina*, *Bakeronymus*, and *Pseudonomadina*.

19. *Propodeal sculpturing*. (0) Areolate-rugose; (1) rugose; (2) punctate; (3) smooth (4) areolate. Shaw (1990), using Ceraphronoidea, Evanioidea and Trigonalyidae as outgroups, found that the primitive state for megalyrids is areolate-rugose, as is found in *Orthogonalys*. Most trigonalyids are punctate but some are rugose or very smooth. *Bareogonalos* is strongly areolate.

20. *Propodeal foramen*. (0) Low 'U' shape (wider than high); (1) high 'U' shape (at least as high as wide); (2) 'V' shape (acute angle at apex). In most evaniomorphs the foramen is 'U' shaped, but it is also closed ventrally, while in all the Trigonalyidae it is open ventrally, so comparison with these taxa may not be useful. However, within the Trigonalyidae the propodeal foramen of *Orthogonalys* is a low 'U' shape, and there appears to be a transition from a low 'U'-shaped to 'V'-shaped foramen. The evaniomorph outgroup was coded as unknown and the ancestral trigonalyid outgroup was coded as a low 'U' shape.

21. *Propodeal foramen carina*. (1) Thick and double-walled; (2) narrow and single walled. Several taxa, including *Orthogonalys*, *Pseudogonalos*, *Bareogonalos*, and an undescribed genus from Papua New Guinea have a thick double-walled carina

while most taxa have a thin carina. The carina in the evaniomorphs does not appear analogous and the ancestral state is considered unknown.

22. _Tergal_ _plate_ _thickness_. (0) Thin, with transparent to translucent edges folding over sterna; (1) not thin, and meeting sterna laterally with little overlap. Several evaniomorphs and _Orthogonalys_ have very thin metasomal plates. Their terga overlap the sterna ventrally, and are distinctly transparent not just at the very margin but over a wide area. _Bareogonalos_, _Nomadina_, and _Pseudonomadina_ also have the ancestral condition of thin terga, apparently secondarily.

23. _Metasomal_ _sternum_ _II_ _(male)_. (0) Rounded medially; (1) flattened or concave medially. Most trigonalyids and evaniomorphs have the metasoma rounded ventrally. This character has been used in the past to separate genera which are synonymized herein under _Taeniogonalos_, but are included separately in the cladistic analysis.

24. _Metasomal_ _segment_ _lengths_. (0) Segments II & III subequal in length; (1) segment II slightly longer; (2) segment II approximately long as all following combined. This character was determined using male specimens when possible but generally applies to both sexes. It is difficult to determine in some specimens of taxa (especially _Orthogonalys_) with thin terga that distort during drying. Many evaniomorphs have an elongated first segment, which is unknown among the Trigonalyidae, but most have segments II and III the same length, so the evaniomorph outgroup and ancestor were coded as segments II & III subequal in length.

25. _Female_ _awl_. (0) No awl; (1) awl present. The awl (Yamane & Yamane, 1975, Fig. 16) is apparently unique to the Trigonalyidae, and seems to have evolved after tyloids originated.

26. _Female_ _capsule_. (0) No capsule present; (1) capsule present. In the derived state the terminal and penultimate sterna are flattened and often lyre-shaped, forming a capsule that positions the apical sternum to point anteriorly. No evaniomorphs

have a capsule and the ancestral condition is assumed to be without a capsule. As this character may be linked to armature presence it was experimentally deleted without affecting the outcome of the analysis.

27. _Female_ _armature_. (0) Absent; (1) female armature present in some members. Because of the complexity of this character it is most parsimonious to assume that armature only originated once, and that the groundplan for taxa with more than one state is presence of armature. Armature is variable, i.e. present or absent, in two genera, _Taeniogonalos_ and _Trigonalys_. In the data matrix, _Taeniogonalos_ is divided into several representative species, for each of which armature is not variable. Experimentally coding _Trigonalys_ as "armature absent" did not affect the topology of the strict or majority rule consensus trees. Armature is absent in all evaniomorphs. Those trigonalyid taxa assumed to have secondarily lost their armature have their metasoma more strongly sclerotized ventrally, and often have the second sternum ventrally swollen or expanded.

28. _Sternal_ _armature location_. (1) Present on sternum II; (2) present on sternum III. If the armature is present on sternum III there are usually traces of armature on sternum II, except in _Trigonalys_. To avoid giving the absence of armature additional weight, this character is coded as unknown for taxa that always lack armature, including the ancestor and outgroup taxon. In experiments where character 27 was combined with this character (similarly and simultaneously with characters 8 and 9 being combined) and the ancestral state was 'armature absent' and the unordered derived states were 'armature present on sternum II' and 'armature present on sternum III' the topology of the strict and majority rule consensus trees was unchanged.

29. _Paramere_. (1) Rounded (about as long as wide); (2) elongate (longer than wide); (3) angulate. The parameres are either relatively short and wide, as is the case in _Orthogonalys_ and several Nomadinini; narrow and elongate, as in _Pseudogonalos_, _Trigonalys_, and _Taeniogonalos_; or sharply angled near the base, as in many

Nomadinini. Male genitalia are figured by Tsuneki (1991). The parameres are fused to the basiparamere in Aulacidae, Evaniidae, Gasteruptiidae, and Stephanidae, and though in these taxa the parameres appear about as long as wide, they are not considered comparable. Thus the ancestral and outgroup states are unknown.

30. *Aedeagus*. (1) Cylindrical, not bilaterally flattened, apex capitate; (2) elongate- thin; (3) strongly bilaterally flattened with the tip expanded, 'T' or plough-shaped. In *Orthogonalys*, the aedeagus is rod-shaped and not bilaterally flattened, and the tip is capitate or slightly expanded into a bulb. In *Trigonalys* and *Taeniogonalos*, the aedeagus is elongate-thin, and slightly bilaterally flattened with the tip variously shaped but not capitate. In most Nomadinini it is strongly bilaterally flattened and the tip shaped like a plough or length-wise 'T' shape. In the evaniomorphs, the aedeagus of Gasteruptiidae, Aulacidae, and Evaniidae is cylindrical but not capitate; in Stephanidae it is apically slightly flattened but the shaft is cylindrical. The aedeagus of the ancestor may be assumed to be a simple cylindrical shaft, closest to the condition in *Orthogonalys*, but without further evidence we are considering the ancestral and outgroup states unknown.

Phylogenetic Analysis

The amount of homoplasy in the Trigonalyidae is a challenge to any method of analysis. Some characters that initially appear monomorphic within a taxon, such as the length of the malar space or the presence of a petiolate second submarginal cell, become increasingly variable as more specimens and taxa are studied.

There are at least two phylogenetically significant, structurally complex features that have arisen within the Trigonalyidae: tyloids and metasomal armature. Since some species have armature but do not have tyloids and some species have tyloids but do not have armature, and other species have both, it is necessary to resolve which taxa have secondarily lost or convergently gained these characters. Despite the variety of forms of armature and tyloids, we believe that they are too complex to have arisen more than once. Most taxa that fall within the Trigonalyini have either armature, traces of armature, or a swollen sternum II, which may be a remnant of armature. Based on this evidence we assume that when both states are present within a taxon, the groundplan for that taxon is presence of armature. In the data matrix this assumption only applies to *Trigonalys*, and experimentally changing the coding for *Trigonalys* does not change the results. It is also more parsimonious to assume that the female capsule arose only once and in tandem with the armature. The capsule serves as a guide to point the ovipositor anteriorly, and the armature serves as a brace for oviposition into a leaf (Carmean, 1988, 1991). Experimentally deleting this character also did not change the results.

The results of the phylogenetic analyses are shown in Figs 24-30. Exactly the same 32 trees resulted from using the trigonalyid groundplan (trigonalyid ancestor), the evaniomorph outgroup, or only the trigonalyid taxa. Using the hypothetical ancestor in the analysis resulted in a tree 72 steps long, C. I. 0.597; excluding the single uninformative character, C. I. 0.592. Using the hypothetical outgroup taxon resulted in 4 additional steps (76 steps), reflecting four synapomorphies for the family (Characters 3, 6, 14, and 18), with a consistency index of 0.566 (excluding uninformative characters, 0.560). The large number of trees are partially a result of including several species of *Taeniogonalos* that were previously separated into different genera and are not strongly differentiated. Including only *T. gundlachii* from *Taeniogonalos* resulted in only 17 trees, 71 steps (using ancestral taxon for rooting).

Table 2 compares the classification from Weinstein & Austin (1991), which is primarily based on Schulz (1907a), Bischoff (1938), and Benoit (1952), with the classification proposed in this study, which is based on the results of a cladistic analysis (Figs 24-28). Several taxa within the Trigonalyinae remain with their status uncertain. They do not share the defining characters of the two tribes nor do they have any characters unambiguously uniting them or clarifying their relationships with other Trigonalyinae. Use of scanning-electron micrographs of the tyloids or DNA sequence data may help establish clades including these taxa.

In the consensus trees (Figs 24, 25), the Trigonalyini are paraphyletic with the Nomadinini. This may be in part because several species of *Taeniogonalos* secondarily lack armature. Further study is required to ascertain if *Taeniogonalos* and *Trigonalys* together form a monophyletic group, and what their relationships are to other taxa. With a reduced number of taxa, the bootstrap consensus tree (Fig. 26) generally agrees with the proposed phylogeny, and the Trigonalyini are not paraphyletic.

Successive approximations character weighting (Farris, 1969) provides an objective method of *a posteriori* character weighting when confronted with several equally parsimonious cladograms. Applied to the characters in this study, the successive approximations character weighting reduces the number of equally most parsimonious cladograms from 32 to 12 and increases the consistency index from 0.59 to 0.71 (Fig. 25). Table 3 shows the final weights assigned each character by this procedure. One major difference between the unweighted and weighted consensus trees is at the base: *Teranishia* joins with *Pseudogonalos* in the unweighted tree (Fig. 24) but with an undescribed genus from Japan in the weighted tree (Fig. 25).

One alternative to _Orthogonalys_ being the most primitive of the trigonalyids is that _Bareogonalos_, _Nomadina_, _Pseudonomadina_ and _Bakeronymus_ are the most primitive Trigonalyidae. _Bareogonalos_, _Nomadina_, _Pseudonomadina_ and _Bakeronymus_ share three generalized apocritan traits, flat SAE, symmetrical mandibles, and undivided hind trochantellus, which are absent from most trigonalyids. These four genera are, however, highly derived in other respects, and their 'primitive' character states may have arisen secondarily. If a genus in the _Bareogonalos_-_Nomadina_ group is assigned to a basal position in the Trigonalyidae (Figs 29, 30), then unique trigonalyid characters including the awl, sclerotization of the capsule, and female armature would have to be interpreted as primitive familial characters lost in various lineages. Rerooting the most parsimonious tree so that _Bareogonalos_ is basal gives the unlikely result of the evaniomorph outgroup nesting well within the ingroup (Fig. 29). Alternatively, experimentally constraining the Nomadinini to be basal (= the sister group) to all other Trigonalyidae required three more steps than the most parsimonious tree (Fig. 30).

The tribe Nomadinini now includes several taxa previously treated as separate subfamilies. While the Nomadininae under Schulz's (1907a) and Weinstein & Austin's (1991) classification are a monophyletic group, the other taxa in their classification are either polyphyletic (Lycogastrinae), too narrowly defined (Bareogonaloinae), or at best, paraphyletic (Seminotinae). Removing the unrelated taxa previously placed in the Lycogastrinae and treating these taxa together as a single tribe eliminates these problems.

Keys to Trigonalyidae by Region

Key to the species of Canada and the United States

1. Dorsellum pyramidal, distinctly raised and usually bifid and yellow. Hind trochanters two-segmented. Parasitoids of yellowjackets ...*Bareogonalos canadensis* (Figs 1-5)

- Dorsellum flat. Hind trochanters three-segmented. From solitary hosts 2

2. Dorsellum and propodeum all black (or very dark brown), without light markings. Antenna spindle-form ....*Lycogaster pullata*

- Dorsellum and usually propodeum with light markings. Antenna filiform 3

3. Antennae black with white (or light yellow) band in middle. Metasoma thin, often entire metasoma orange. The only North American species without female armature. Male without tyloids ....*Orthogonalys pulchella*(Figs 6-9)

- Antennae without light-colored band. Metasoma stout, dark, with transverse yellow stripes. Female with armature. The only North American species in which the male has tyloids (Fig. 10) ....*Taeniogonalos gundlachii* (Fig. 17)

Key to New World Genera

1. Tyloids not present, or female. Antennae filiform or thickened 2

- Tyloids present, antennae filiform[1]. (males only) 8

2. Maxillary and labial palpi rudimentary. Antenna 16-segmented ....*Nomadina*

- Maxillary palpus extending beyond mandibles, labial palpus normal. Antenna with 17-28 segments 3

3. Antenna with 17-20 (rarely 21) segments. Metasoma smooth, shiny and thorax strongly areolate. Hind trochanter two-segmented ....*Bareogonalos*

- Antenna with 21-28 segments. If metasoma smooth and shiny then thorax not strongly punctate. Hind trochanter apparently 3-segmented (second segment diagonally divided) 4

4. Metasomal terga and sterna very smooth and thin (may be partially transparent), terga folded under, intercalating with sterna. Propodeum areolate-rugose, covered with network of lines. Carina around propodeal foramen thick, partially double-walled, "U" or half circle shaped. Ichneumonid-like: antenna banded, when viewed dorsally head and thorax black with markings white (females and faded males) or yellowish white (males); metasoma orange, may have extensive light or dark markings ....*Orthogonalys*

- Metasomal terga and sterna often punctate, thick, terga overlap sterna laterally in a straight line, without overlapping sterna ventrally. Propodeum punctate, or smooth, sometimes with concentric lines around foramen, but not covered with network of lines. Carina around propodeal foramen thin (though sometimes tall), and 'V' or 'U' shaped. Coloration various, not as above 5

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[1]One male from Costa Rica has antennae like *Lycogaster* but with tyloids, the rest of its characters as in Trigonalyini.

5. Eye with sparse pubescence visible at 30 X. Eye in lateral view often with posterior margin behind mandibular insertion (Fig. 32). Propleuron and mesopleuron yellow and entire forewing pale amber; in some species vertex behind ocelli flat, posteriorly abruptly angled towards genal carina; propodeal foramen evenly curved dorsally. Very rare in collections ....*Xanthogonalos*

- Eye not pubescent. Eye with posterior margin even with middle of mandibular insertion (Fig. 31), less commonly at posterior edge of mandibular base. Propleuron dark, mesopleuron dark or dark with yellow markings (except *Taeniogonalos* *ornata* and some *Trigonalys*, which also have only the leading half of the forewing pale amber) 6

6. Antenna spindle-shaped. No yellow or light markings on propodeum. Supra-antennal elevation reduced, never lobed. Frons between antennae broad and flat, wider than the length of the first flagellomere. Tyloids absent 7

- Antenna filiform. Often with yellow on propodeum. Supra-antennal elevation variable. Frons between antennae usually narrower and not flat. Tyloids present in male 8

7. Wings amber or hyaline, not very dark. Head punctate, vertex curving evenly towards occipital carina. Parasitoids of solitary wasps and of parasitoids of Lepidoptera ....*Lycogaster*

- Wings, or part of wings, very dark or violaceous. Head smooth, vertex sharply angled above occipital carina. Parasitoids of social wasps ....*Seminota*

8. Genal carina not forming a sharp ridge between gena and occiput, occiput not sharply excavated (Fig. 23). Frons flat or slightly angled between antennae in side view. Punctate above clypeus. Gena usually narrow (Fig. 31), often punctate, immediately above mandible and behind lower third of eye. Female armature, if

present, on sternum II. Male tyloids elongate, usually more than half flagellomere length ....*Taeniogonalos*

- Genal carina forming a sharp ridge between gena and occiput when viewed from below; occiput usually sharply excavated all the way to mandible (Fig. 22). Frons strongly angled between antennae in side view. Glossy above clypeus between antennae. Gena wide and shining immediately above mandible and behind lower third of eye. Female armature, if present, on sternum III. Male tyloids oval or round, less than half the flagellomere length 9

9. Genal carina pointing towards hypostomal carina and then bending parallel to hypostomal carina to reach mandibular base. Occiput not sharply excavated near mandible. Mexico, known only from females ....Undescribed Genus

- Genal carina extending straight to mandibular base. Occiput sharply excavated along genal carina all the way to mandible. Central and South America ....*Trigonalys*

Key to African Genera

1. Antenna banded. Propodeum, at least above propodeal foramen, rugose reticulate (wrinkled network). Genal carina fading before hypostomal carina, not ending at mandibular base. Males without tyloids. Wings hyaline, submarginal cell II petiolate to subpetiolate. Mesosoma predominately orange. Metasoma without armature. Metasomal plates thin and may dry distorted ....*Orthogonalys*

- Antennae not banded. Other characters various, but not fitting above description. Wings often with dark markings; females often with armature; males often with tyloids 2

2. Area immediately above clypeal suture smooth and shiny- not punctate. Frons usually with strong ledge between antennae. Gena wide (Fig. 33), genal carina at top of genal angle (Fig. 22). Thorax and abdomen predominately black, tergum II often with ivory diagonal markings or all black. Female armature various, usually present. Wings darkened or smoky ....*Trigonalys*

- Area immediately above clypeal suture as punctate as frons immediately above antennae. Frons relatively flat. Metasoma dark with transverse light markings or entirely orange. Female armature on sternum II. Other characters variable 3

3. Shortest distance between toruli (antennal sockets) about the same as the shortest distance between the inner eye margin and the torulus. Marginal cell and area distal of marginal cell much darker than discal cell. Female with bluntly bifid armature on sternum II, armature on sternum III forms a flat ledge under sternum II and does not project. Male with flattened sterna and with 5 or more narrow elongate tyloids on outside of antennae ....*Taeniogonalos*

- Shortest distance between toruli is almost twice the shortest distance between the inner eye margin and the torulus. Wing hyaline or evenly colored, marginal cell not darker than rest of wing. Metasoma orange except darker near petiole. Female armature with two parallel sharp 'fins' on sternum II, armature on sternum III forms a flat projecting ledge under sternum II. Male unknown, possibly without tyloids ....*Afrigonalys*

Key to Eurasian and Indo-Australian Genera[1]

1. Vertex cleft at midline. Antennae with 13-15 segments 2
- Vertex normal. Antennae with 17-32 segments 3

2. Maxillary palps rudimentary ....*Pseudonomadina*
- Maxillary palps about as long as mandibles and distinctly segmented .....*Bakeronymus*

3. Males (with parameres which appear as paired paddle-shaped appendages sometimes projecting ventrally from abdomen and not to be confused with cerci(?), which are dorsal, short and rounded; tyloids may be present on antennal segments 10 through 13-18; never with medial projection at or near apex of sternum II or III, though sternum II sometimes with a projection on the anterior half before a flattened area in *Taeniogonalos*, or with two small pre-apical lateral spines in *Lycogaster*) 4
- Females (often with armature, never with tyloids on several flagellomeres, but flagellomeres always with, though not always visible, a circular area of white spots in same location as tyloids are on male) 11

4. Tyloids absent 5
- Tyloids present 7

[1]Europe has only one species, *Pseudogonalos hahnii*. The key excludes Tsuneki's genera *Taiwanogonalos*, *Jezonogonalos*, and the males of *Teranishia*.

5. Terga opaque where they overlap sterna laterally, not folding over sterna ventrally. Sternum II with two small pre-apical spines, just lateral of midline. Vertex rounded ....*Lycogaster*

- Terga with wide translucent to transparent lateral margins that reach ventrally and overlap sterna. Sternum II without ventral spines. Vertex flat and rectangular 6

6. Stout bodied, Vespine-like. Thorax strongly areolate. Antennae not banded, sometimes thickened, with 18-23 segments ....*Bareogonalos*

- Body slender and elongate, ichneumonid-like. Thorax sparsely punctate. Antennae filiform, often banded, with 22-32 segments. Metasoma thin, and generally tubular ....*Orthogonalys*

7. Tyloids linear ....*Taeniogonalos*

- Tyloids not linear but broadened or rounded 8

8. Tyloids almost round, globular shape 9

- Tyloids oval-elongate. Gray color, with dull luster 10

9. Genal carina ending at lateral edge of mandibular base. Frons forms a horizontal 'shelf' between antennae, the line from the median ocellus to the clypeus strongly angled in side view. No large vertical lobes over scape ....*Trigonalys*

- Genal carina ending at hypostomal carina. Frons medially flat, with large vertical lobes covering the scape ....*Pseudogonalos*

10. Tyloids with broad flat top surface, with dull velvet like luster ....Genus 2

(Two undescribed species from New Guinea)

- Tyloids keel shaped, top surface not flat, with dull lead-like luster. Australia ....*Mimelogonalos*

11. Distinct armature present on second or third metasomal sternum 12

\- Armature not present 16

12. Armature only on sternum III 13

\- Armature on sternum II, if also on sternum III, smaller and covered by armature on sternum II 14

13. Gena smooth, shining. Frons strongly angled in side view ....*Trigonalys*

\- Gena punctate. Frons relatively flat ....*Taeniogonalos flavocincta*

14. Top of head rectangular, flattened. Sternum III with small posteriormedial projection often under sternum II. Propodeum strongly areolate, metasoma generally smooth and usually shining ....*Bareogonalos*

\- Top of head rounded, not flattened. Sternum III may form a ledge but does not project posteriorly. Propodeum not strongly areolate, metasoma various, often punctate and dull 15

15. Armature consisting of flat vertical ledge at apex of sternum II with two small indistinct lateral spines slightly more raised than the center ledge. The anterior part of sternum III forms a wide but not very tall ledge under sternum II. Antennae spindleform ....*Lycogaster*

\- Armature various but not as above. Antennae filiform ....*Taeniogonalos* (in part)

16. Supra-antennal elevation reduced, intertorulus area is relatively flattened, without projecting lobes. Toruli (bases of antennae) as far apart as length of first flagellomere. Propodeal foramen usually 'V' shaped, taller than wide, with a weak, thin carina around it. Sternum II swollen ventrally and may have slight medial elevation in front of posterior edge. Terminal sternum pointing anteriorly toward sternum II or straight down; tip sclerotized, forming short hypodermic needle-like structure ....*Taeniogonalos* (in part)

- Supra-antennal elevation prominent, often forming distinct lobe. Intertorulus distance variable, often close together. Propodeal foramen usually 'U' shaped, generally wider than tall and usually bordered with a thick carina. Sternum II not swollen ventrally and without medial elevation. Terminal sternum in undistorted specimens pointing down or posteriorly, usually not more sclerotized at tip than rest of sternum 17

17. Genal carina ending at lateral edge of mandibular base. Terminal sternum modified into cylindrical tube generally pointing straight down ventrally. Mesosoma and metasoma compact, not elongate. Australia ....*Mimelogonalos*

- Genal carina ending at hypostomal carina. Terminal sternum not cylindrical, generally pointing straight back posteriorly. Body elongate. Not known from Australia 18

18. Propodeal carina 'U' shaped, foramen 'V' shaped 19

- Propodeal carina and foramen both 'U' shaped 20

19. Frons with large shiny vertical lobes mesad of the scape that are generally all black ....*Pseudogonalos*

- Frons with punctate lobes, not shiny, and generally with light markings ....*Teranishia*

20. Dorsellum pyramidal. Petiole strongly constricted and distinctly different from second metasomal segment. Tergum II much longer than tergum III. Wings hyaline, infuscate, or fasciate ....Genus 2 (New Guinea)

- Dorsellum flat. Petiole not constricted, sternum I similar to sternum II. Tergum II slightly longer than tergum III in undistorted specimens. Wings hyaline ....*Orthogonalys*

TRIGONALYIDAE CRESSON 1887

Trigonalidae Cresson 1887: 183.

Trigonalyidae Krieger 1894: 23.

Förster (1877) placed *Trigonalys* alone in the taxon 'Diplomorpha' which was treated equivalently to other Hymenoptera now recognized as families. Cresson (1887) was the first to use *Trigonalys* to form a family-rank name but this was apparently overlooked by others. Bischoff (1938) attributed the family to Krieger (1894), but the Trigonalyidae should be attributed to Cresson (1887). Many spelling variants have been proposed (Bischoff 1938, Weinstein & Austin 1991) due to the ambiguity of the root of *Trigonalys*. Eight years after naming the genus Westwood (1843) wrote that the "genus is named in allusion to the triangular form of the second submarginal cell" but does not provide the information required to determine if the root is Trigonal- or Trigonaly-.

ORTHOGONALYINAE (Subfamilia N.)

Type genus: *Orthogonalys* Schulz 1905

***Orthogonalys* Schulz**

Orthogonalys Schulz 1905: 76. Type species *O. boliviana* Schulz 1905 (by monotypy), repository: ZSMC. *Orthogonalos* Schulz 1907a (unjustified emendation).

Tapinogonalos Schulz 1907a: 14. Type species *Trigonalys pulchella* Cresson 1867 designated by Viereck (1914), lost (Cresson, 1916). (**Syn. n.**)

Satogonalos Teranishi 1931: 10. Type species *S. debilis* Teranishi by original designation, OMNH (Tsuneki, 1992). Synonymy by Tsuneki (1991).

Diagnosis

Body slender, elongate; length 3.5-14.1 mm; FW 3.5-13.5 mm, most species approximately 9 mm long, FW 8 mm. Genal carina mesad of sharp genal angle, reaching or fading away before hypostomal carina; gena smooth, narrow behind eyes and generally strongly angled in ventral view; malar space generally long; antennae long, filiform, with 21-32 (most species 26-28) segments, often banded, tyloids absent; toruli close together: shortest distance between toruli less than 0.9 times the shortest distance between the inner eye margin and the torulus; wings hyaline, submarginal cell 2 often petiolate; propodeal foramen low, 'U' shaped, with wide carina; metasomal terga II & III roughly the same length (distortion of the thin plates occurs); tergum II generally with posterior medial indentation; terga mostly thin and transparent, wrapping ventrally over sterna. Aedeagus with capitate tip; parameres various, generally not much longer than wide; sterna flat, female without armature or ventral swelling and not strongly sclerotized.

Discussion

Orthogonalys contrasts with most other trigonalyids in several ways. Members of this genus are slender and delicate, with hyaline wings, and often banded antennae (Fig. 6). New World and African species have either their metasoma or mesosoma, or both, mostly orange, and the remainder of the body black and white. Asian species are mostly black with some white or brown markings. The outgroup analysis shows *Orthogonalys* is defined by primitive rather than derived characters.

Orthogonalys has a greater number of the ancestral apocritan characters than other trigonalyid genera. Like the presumed primitive evaniomorph, *Orthogonalys* has areolate-rugose propodeal sculpturing, an elongate body form, thin metasomal terga that fold ventrally and overlap the sterna, a long malar space, and a genal carina ending near the hypostomal carina (rather than at the mandibular base). *Orthogonalys* cannot be assigned any unique, derived characters partly because the available outgroups are too distant to provide information about ancestral character states. Male *Orthogonalys* lack tyloids. The metasoma of female *Orthogonalys* is unsclerotized, lacks armature or traces of armature, and lacks modifications for piercing and oviposition in leaves.

Schulz (1905) described _Orthogonalys_ as having only 5 maxillary palps, when in fact they have six. Schulz (1907a) also characterized the genus as having the metasomal terga "klaffend" or wide apart at the lateral posterior edges. However, this is a sexually dimorphic character in _Orthogonalys_. Females have a broad, generally flattened metasoma (Fig. 8), which is not much longer than wide, and is wider than the thorax. Schulz, deceived by the dimorphism, placed males in a different subfamily, because of their elongate, almost tubular, metasoma, which is narrower than the thorax (Fig. 7). The lightly sclerotized metasomal plates are easily distorted, which adds to the confusion.

The genus _Orthogonalys_ includes some of the longest and some of the shortest bodied Trigonalyidae. _Orthogonalys_ _centrimaculta_ is known from a single specimen collected from northern Vietnam and is among the longest trigonalyids: the body is 14.1 mm long and the forewing is 13.5 mm long. In _Orthogonalys_ size varies greatly within a species. One female _O_. _formosana_ is 9 mm long [TARI] while another female of the same species is only 3.5 mm long [AEIC].

Because of the intra-specific variation in size and wing venation as well as the sexual dimorphism and possible abdominal distortion due to the thin metasomal plates, some of the species described from individuals or short series are probably synonymous. _Orthogonalys_ _gigantea_ appears to be a large _O_. _hova_. Tsuneki (1991) discussed the similarities of _O_. _fukuiensis_ with _O_. _elongata_ as well as the confusion caused by variation within _O_. _elongata_.

Tsuneki (1991) suggested that _O_. _formosana_, which he knew only from the holotype description, may represent an undescribed genus, while our study shows that the species shares all the features of _Orthogonalys_. _Orthogonalys formosana_ is the only _Orthogonalys_ from Asia with the following characters: hind femur and base of hind tibia amber, remainder of hind tibia dark brown; opaque white parameres (parameres of all other Trigonalyidae we have seen are dark to amber); and the midline of thorax and propodeum with white spots of varying size and intensity. _Orthogonalys formosana_ is known only from Taiwan. *Orthogonalys debilis* (limited to Japan) has light markings on the scutellum and dorsellum but the hind femur is dark and there are no light markings on the midline of the propodeum. A species of *Lycogaster* from Java has the mesonotum similarly marked but it would not be confused with *Orthogonalys*. While the holotype has the mandibles each with four well-developed mandibular teeth, this is not normal for the species. Symmetrical mandibles have been seen in individual *O. boliviana* and other species with typically asymmetrical mandibles.

Some trigonalyids in other genera may appear similar to species of *Orthogonalys*. *Taeniogonalos maga* (Teranishi) resembles dark *Orthogonalys* but lacks the thin metasomal terga, and has tyloids. The propodeal foramen of *Taeniogonalos* is 'V' shaped, while in *Orthogonalys* it is squat and generally 'U' shaped. *Afrigonalys* species may also resemble *Orthogonalys* but has female armature and does not have banded antennae. The toruli are far apart and the SAE are less prominent in *Taeniogonalos* and *Afrigonalys* than in *Orthogonalys*. The SAE are generally lobed and projecting in *Orthogonalys* but in the North American species *O. pulchella* the SAE may be reduced.

We are synonymizing *Tapinogonalos* under *Orthogonalys* because Viereck (1914) designated *Trigonalys pulchella* as the type species of *Tapinogonalos* and Bischoff (1938) transferred *Trigonalys pulchella* to *Orthogonalys*. Bischoff (1938), unaware of Viereck's designations, designated the unrelated *Tapinogonalos maschuna* Schulz as the type species of the genus. *Tapinogonalos* is thus a junior synonym of *Orthogonalys*.

Distribution

There are two disjunct but closely related New World species, *O. pulchella* in North America (eastern United States, Mexico, and Canada) and *O. boliviana* in South America (Bolivia, Brazil, Argentina, Peru). In the Old World the genus is well-represented in Japan. Several *Orthogonalys* species known from one to a few specimens come from eastern Africa and Madagascar, northeastern India, northern Vietnam, and Taiwan.

Biology

Smith (1996) discusses the seasonal flight activity of *O. pulchella*. In North America, the records of *O. pulchella* parasitizing *Nilea* (=*Zenillia*) *lobeliae* (Tachinidae) in *Acronicta lobeliae* (Noctuidae) (Bischoff, 1909; Townes, 1956; Weinstein & Austin, 1991) are incorrect and result from taxonomic confusion. Schulz (1907a) synonymized *O. pulchella* with *Trigonalys costalis* Cresson (=*Taeniogonalos gundlachii*), and then reported Riley & Howard's (1891) rearing of *T. gundlachii* as a host record from *O. pulchella*. Bischoff (1938) correctly attributed this rearing record to *T. costalis* (=*gundlachii*) when he removed *O. pulchella* from synonymy with *T. costalis*. However, according to Carlson (1979) *O. pulchella* has been reared from Tachinidae parasitizing Lepidoptera. *Orthogonalys seyrigi* was reared from a limacodid moth, which was presumably its intermediate host (Benoit, 1951).

Species included

Orthogonalys albomaculata Bischoff 1951. Examined 4 from INDIA (BMNH*).

Orthogonalys boliviana Schulz 1905. Examined from South America (44 AEIC, 3 CNCI, 5 BMNH, ZSMC*).

Orthogonalys centrimaculta Bischoff 1951. Examined 4 from VIETNAM (BMNH*)

Orthogonalys elongata Teranishi 1929.
=*Orthogonalys hirasana* Teranishi 1929 (syn. by Marsakov 1981).
=*Orthogonalys debilis* Teranishi 1929 (syn. by Tsuneki 1991).
Examined from JAPAN (39 AEIC, 5 CNCI).

Orthogonalys formosana Teranishi 1931. Examined 104, 32 from TAIWAN (AEIC, TARI, UOPJ*).

Orthogonalys fukuiensis Tsuneki 1991.

Orthogonalys gigantea Benoit 1951.

Orthogonalys hagoromonis Teranishi 1929. Examined 127 specimens from JAPAN (AEIC, CNCI).

Orthogonalys hova Bischoff 1933. Examined 14, 32, 1? from MADAGASCAR, TANZANIA (AEIC, MRAC, NHMW, ZMUC).

Orthogonalys pulchella (Cresson 1867). Numerous specimens from eastern North America. (USNM, CNCI, AEIC, ZSMC, TAMU, CASC, FSCA, others).

Orthogonalys seyrigi Bischoff 1933. Examined 2 from TANZANIA (tentative identification, species described from Madagascar)(AEIC).

TRIGONALYINAE CRESSON 1887

The subfamily Trigonalyinae, unlike the Orthogonalyinae, comprises all taxa possessing tyloids. The tribe Nomadinini, within the Trigonalyinae, is assumed to have lost tyloids secondarily. Previously this subfamily was characterized by the absence of female armature (Schulz, 1907a) and included all such taxa (+ *Discenea*!?). According to the current analysis, female metasomal armature is not part of the groundplan for the family and has been lost repeatedly within the tribe Trigonalyini. Thus the presence or absence of metasomal armature is not by itself a distinguishing character for any monophyletic group. Schulz (1905) and Bischoff (1938) attributed the Trigonalyinae to Cameron (1899) who stated that he was establishing a new tribe and then gave the diagnostic features of "Trigonalidae" (?misspelling for Trigonalini) and "Nomadinae" (?misspelling for Nomadininae or Nomadinini). Apparently because of the confusion surrounding the spelling and ranking of Cameron's groups, Weinstein & Austin (1991) attributed the name to Schulz (1907a). However, since all family-group names are equivalent in status, the first used family-group name takes precedence for all family-group names (International Commission on Zoological Nomenclature, 1985, article 36a). Thus Cresson (1887), even though he never used the name Trigonalyinae at the subfamily level, is the correct author of this subfamily.

Several genera in the Trigonalyinae, including *Pseudogonalos* and *Mimelogonalos*, have not been included in any tribe. This approach was taken because they do not the possess the apomorphies defining the two tribes and, further, they have no characters uniting them beyond those of the subfamily. Some specimens, possibly representing undescribed genera, require additional specimens for satisfactory description and placement. A single undescribed female from Japan (Genus 1 in data matrix, Table 1, CNCI) has an unsclerotized structure that appears similar to a capsule. This specimen is close to *Orthogonalys* in most other respects (thin overlapping metasomal plates, genal carina ending before hypostomal carina, and hind trochantellus divided), except for a strongly areolate propodeum similar to that of *Bareogonalos*. A partial fusion of metasomal terga I & II is unique to this specimen. The male, and whether it has tyloids, is unknown. Because the 'capsule' is not sclerotized and the specimen does not have other derived features in common with the taxa that have capsules, we do not consider it homologous with a capsule. However, in the data matrix it has been conservatively coded as being a capsule. Two unidentified species from New Guinea (Genus 2, BPBM, AEIC, BMNH) with some primitive characteristics of *Orthogonalys*, such as the terga thin and folding ventrally, have broad elongate tyloids similar to, but not the same as *Mimelogonalos*. These taxa, as well as *Teranishia* are all placed in the Trigonalyinae. More work on the Asian fauna is required to develop a more satisfactory understanding of the basal relationships within the Trigonalyidae.

Nomadinini Cameron 1899

Type genus: *Nomadina* Westwood 1868

Diagnosis

Body shape variable but never appearing slender and delicate. Antennal segments generally thickened; tyloids never present; shortest distance between toruli 1.7-2 X the shortest distance between inner eye margin and torulus; SAE is reduced and the intertorulus area is generally very flattened; genal carina reaching or ending immediately before mandibular base; metasomal plates often strongly sclerotized; female metasomal armature always present on sternum II and usually with a with a reduced armature on sternum III, sometimes under the projection of sternum II; parameres variable but generally elongate.

Discussion

The genera in this tribe are characterized by the females with the primary armature ordinarily on sternum II and secondary armature on sternum III, and the males with a secondary loss of tyloids. All parasitize social wasps, except *Lycogaster* which parasitizes both ichneumonids attacking Lepidoptera and solitary wasps (Eumeninae). Hosts are unknown for *Afrigonalys* and *Xanthogonalos*.

Bakeronymus, *Nomadina*, and *Pseudonomadina* form a distinctive monophyletic group (the old subfamily Nomadininae) (Fig. 27) having only rudimentary armature on sternum II, and their primary armature on sternum III. They also have short rounded parameres. These genera group with *Bareogonalos* based on their undivided hind trochantellus and symmetrical mandibles, although not all *Bareogonalos* have symmetrical mandibles. *Bakeronymus* and *Pseudonomadina* are sister groups sharing many complex derived features as well as having an overlapping distribution. These genera both have the vertex concave and the antenna low on the face, adjacent to the mandible. *Nomadina* and *Pseudonomadina* have rudimentary maxillary palps, but this appears to be convergent based on cladistic analysis. Another interesting, apparently convergent character is the contraction of the head posteriorly into a neck (Fig. 35) in both the _Bakeronymus_ _typicus_ Rohwer female from Taiwan and in _Nomadina_ _cisandina_ Schulz. It is not found in the _B_. _typicus_ male from the Philippines or in any other _Nomadina_ (Fig. 36).

Afrigonalys (gen. n.).

Type species: _Tapinogonalos_ _erythromelaina_ Benoit 1951; holotype repository, MRAC.

Diagnosis (female only)

Length: 6-9.2 mm, FW 6.7-7.4 mm. Genal carina ending at mandibular base; malar space short; gena behind base of eye swollen and extending in a transverse plane out from the genal carina; gena and vertex shiny, punctures and pubescence sparse; antennae filiform; toruli set far apart, shortest distance between inner margins of the toruli almost twice the shortest distance between the inner eye margin and the outer edge of the torulus; maxillary palps longer than mandibles; propodeal foramen 'V' shaped bordered by a narrow carina; tergum II about as long as remaining terga; armature with two parallel, sharp 'fins' on sternum II, armature on sternum III forming a flat ledge under sternum II; genitalia in flattened capsule, pointing towards armature. Male unknown.

Discussion

The vertex of _Afrigonalys_ is tall and rounded, and its surface, as well as that of the genae, is shiny and smooth. Species of _Afrigonalys_ are black and orange with white markings. The metasoma in _Afrigonalys_ _ornatissima_ and _Afrigonalys_ _erythromelaina_ is orange except near the petiole. _Afrigonalys_ _ornatissima_ is white on the scutellum and the middle of the dorsellum, with extensive white markings on the head, resembling _Orthogonalys_ _seyrigi_ and suggesting they mimic a third wasp. The head and mesosoma of _Afrigonalys_ _erythromelaina_ is all black except for the mandibles and a small intra-orbital white mark. In both species the orange metasoma with thin terga, elongate shape, and shiny head create a superficial resemblance to *Orthogonalys*. However, *Orthogonalys*, has a narrower space between the toruli than *Afrigonalys*, and *Orthogonalys* females lack armature that is present in *Afrigonalys*. *Afrigonalys* also resembles *Trigonalys rufiventris* but it does not have the typical *Trigonalys* ledge between the antennae. *Afrigonalys semirubra* has an orange-brown head and thorax and black metasoma with ivory markings. *Taeniogonalos* species have a punctate, dull vertex.

Based on the phylogenetic analysis, *Afrigonalys* is basal to the rest of the Nomadinini. Characters uniting *Afrigonalys* with the Nomadinini include the flat area between the reduced SAE, intertorulus distance greater than eye to torulus distance, and the presence of female armature and capsule. Male *Afrigonalys* are unknown, and *Afrigonalys* males may, like the rest of the Nomadinini, lack tyloids. The position of *Afrigonalys* in the phylogenetic analysis remains unchanged even if the missing antennal character is experimentally coded as "linear tyloids present."

Etymology

The name of this genus is derived from the Latin for dwellers in Africa combined with the common ending for trigonalyids as originally spelled by Westwood.

Distribution

This genus is only known from South Africa, Zaire, and Zimbabwe.

Biology

Unknown.

Species included

Afrigonalys erythromelaina (Benoit 1951). Transferred from *Tapinogonalos*. (**comb. n.**). Examined 2 from ZAIRE (MRAC*).

Afrigonalys ornatissima (Benoit 1950). Transferred from *Tapinogonalos*. (**comb. n.**). Examined 2 from ZAIRE (MRAC*).

Afrigonalys semirubra (Bischoff 1913b). Transferred from *Tapinogonalos*. (**comb. n.**). Examined 2 from SOUTH AFRICA (ZMHB).

Bakeronymus Rohwer

Bakeronymus Rohwer 1922: 417. Type species _B_. _typicus_ Rohwer 1922 (by monotypy), repository: USNM.

Diagnosis

Body elongate, dark reddish brown with extensive yellow markings, length 7.7-9.5 mm, FW 6.1-8 mm. Head wide, rectangular both in anterior and dorsal view, width 2.8 X length, measured from hind edge vertex to front of median ocellus, strongly cleft at vertex; entire head smooth and shining; antenna adjacent to mandible, clypeus between antennal insertions; maxillary palps very short, approximately length of mandible, four-segmented (first segment short); malar space short, at least in male; genal carina indistinct, ending at mandibular base; mandibles symmetrical, basal tooth wide, almost as wide as the 3 remaining teeth; antenna 14-15 segmented, first two flagellomeres elongate and thin, remaining flagellomeres thicker and cylindrical, not beadlike; antennal insertions wide apart, intertorulus distance is about 2.5 times the shortest distance between the inner eye margin and the torulus; wing with marginal cell darkened; two closed submarginal cells (the one female examined has part of 3rs-m cross vein); propodeal spiracle not covered; metasoma spatulate, petiole laterally slightly flattened. Parameres in side view short, 0.2 X length of basiparamere, and as wide as basiparamere; aedeagus not clearly visible, but appears elongate as in _Pseudonomadina_; female sternum I indented apicomedially, sternum II similarly indented but sclerotized and appearing like small bifid tooth or rudimentary armature; sternum III with prominent bifid armature projecting over smaller armature on sternum IV, and out over terminal sternum; genitalia enclosed in capsule and tip of metasoma modified into a sharp hollow awl.

Discussion

The distinctive head immediately distinguishes this genus from all other Trigonalyidae except the closely related *Pseudonomadina*. The head is shiny, transverse, with the midline at least slightly concave from the back of the vertex to the clypeus. The antennal insertions are adjacent to the mandibular base, and the clypeus is situated between the antennae. The easily visible maxillary palps that are about as long as the mandibles will distinguish this genus from *Pseudonomadina*, which has vestigial palps. An anterior view of the head is given in Yamane & Kojima (1982). In dorsal view the female from Taiwan has a distinct neck, as in Fig. 35, that is not found in the male from the Philippines. Unfortunately, the only specimens known are two males from the Philippines and four females from Taiwan, and the variation may be due to sexual or geographic variation, as well as species differences (Yamane & Terayama, 1983).

Distribution

Bakeronymus has been collected in the Philippines and Taiwan.

Biology

The genus was reared in Taiwan from *Parapolybia varia* Fabricius (Polistini, Vespidae) (Yamane & Terayama, 1983).

Species included

Bakeronymus typicus Rohwer 1922. Examined 4, 2 from PHILIPPINES, TAIWAN (USNM*, YAMA).

***Bareogonalos* Schulz**

Bareogonalos Schulz 1907a: 18. Type species *Trigonalys canadensis* Harrington 1896, designated by Schulz (1907b) *nec* Viereck (1914). Repository: ZMHB, see Carmean, 1989.

Nippogonalos Uchida 1929: 79. Type species *N. jezoensis* Uchida 1929 by monotypy, repository: EIHU (Yamane, 1973).

Diagnosis

Mesosoma and metasoma stout and thick; body length: 8.3-13+ mm (forewing 7.5-13.1 mm); head small and rectangular, with long pubescence; malar space long; genal carina obsolescent near hypostomal carina; antenna 18-23 segmented; intertorulus distance variable, usually about equal to torulus to inner eye distance, half as wide in *B. huisuni* and an undescribed species from Sumatra; mandibles symmetrical (except in *B. jezoensis*); scutellum raised; hind trochantellus undivided; thorax and propodeum coarsely areolate, contrasting with smooth, generally shining metasoma; terga transparent at sides; metasoma sexually dimorphic, in female almost as high as wide, semi-rectangular and blunt posteriorly in dorsal view, in male elongate fusiform, pointed posteriorly; paramere is short and wide, forming right angle to basiparamere, width 3.3 X length and 1.3 X width basiparamere; aedeagus laterally flattened, expanded at tip into symmetrical club or 'T', width 3.6 X width of base, each side of 'T' about the same height as width of base. Female primary armature on sternum II, projects over sternum III which has a similarly shaped though slightly smaller armature; genitalia held in capsule.

Discussion

The species of *Bareogonalos* form a monophyletic group united by their parasitism of vespines, and by their dorsally transverse heads with long pubescence, generally stout shape, sexual dimorphism, deeply areolate propodeum and smooth, often shining metasoma. The female metasoma is almost as high as it is wide with the main armature on sternum II. *Bareogonalos* has the hind trochantellus undivided and maxillary palps as long or longer than the mandibles. The antennal insertions are above the clypeus, remote from the mandibular base. Other genera with the hind trochantellus undivided have relatively slender metasomas with the main armature on sternum III. These other genera also have greatly modified heads including vestigial palps and/or antennal insertions at the level of the mandibular base with the clypeus between the insertions.

Koenigsmann (1976), apparently based on Schulz (1907a), stated that *Bareogonalos* females characteristically have one more antennal segment than the males. However, the number of flagellomeres depends primarily on the size of the individual, and thus the host size (Carmean, 1988; Yamane & Yamane, 1975).

Distribution

Species of *Bareogonalos* are found around the perimeter of the Pacific including SW Mexico, NW United States and SW Canada, E Siberia, Japan, Taiwan, and Indonesia (Java and Sumatra).

Biology

Bareogonalos species are the only confirmed trigonalyid parasitoids of Vespinae (Vespidae), including *Dolichovespula*, *Vespa*, and *Vespula* (Carmean, 1988, 1991; Carmean *et al*., 1981; Ono, 1987, 1988; Stage & Slobodchikoff, 1962; Vecht, 1934; Yamane, 1973; Yamane & Yamane, 1975). In addition, an undescribed species from Indonesia was reared from *Provespa* (YAMA).

Species included

Bareogonalos canadensis (Harrington 1896). Examined numerous specimens from CANADA and USA (CARM, CASC, CNCI, USNM, ZMHB*).

Bareogonalos huisuni Sk. & S. Yamane 1975. Examined 12, 1? from TAIWAN (YAMA).

Bareogonalos jezoensis (Uchida 1929). Examined 34, 42, from INDONESIA and JAPAN (ZMHB, MCZC, USNM, CARM).

Bareogonalos scutellaris (Cameron 1897). Examined holotype 4, and holotype 2 of *Trigonalys flavonotata* Cameron 1897, from MEXICO (BMNH*).

Undescribed *Bareogonalos* sp. from INDONESIA, 4, 2 (YAMA).

Lycogaster **Shuckard**

Lycogaster Shuckard 1841: 121. Type species *L. pullata* Shuckard 1841 (by monotypy), repository: lost.

Diagnosis

Body stout, length 5.5-13 mm, FW 4.8-11.2 mm (most 9-10 mm long, FW 8.5 mm). Genal carina meeting lateral edge of mandibular base in Asian species and hypostomal carina in New World species; malar space short; antenna spindleform or thickened, with 22-24 segments, lacking tyloids; shortest distance between toruli 1.7-2 X the shortest distance between inner eye margin and torulus; anterior tentorial pits large; clypeal suture (=epistomal suture) indistinct; forewing with submarginal cell II ordinarily not petiolate; entire forewing smoky (not dark); tergum I relatively broad; tergum II about as long as following terga together. Paramere making almost a forty-five degree angle to basiparamere, and short and wide (2.7 X wider than tall); basiparamere 1.7 X longer than wide; aedeagus laterally flattened, tip drawn out to a dorsal point, height of tip 1.25 X the height of shaft; anterior transverse groove on sterna III & IV of male; female sternum II with high posterior ledge, central projection distinct in New World species and slight in Asian species, sternum III with anterior ledge, often under ledge of sternum II.

Discussion

Lycogaster can be identified by the stout, usually punctate body, and the short spindleform antenna with the flagellomeres cylindrical rather than knobbed as in *Bareogonalos*. The second metasomal segment is longer than the following segments which are slightly attenuated and in the female, strongly curved ventrally and anteriorly. The female armature is composed of a ledge on the second sternum which does not project posteriorly over the following segments. *Lycogaster* may be most closely related to the neotropical genus *Seminota*. However, *Seminota* species have shiny heads with long, posteriorly angulate vertices, while those of *Lycogaster* have punctate heads with rounded vertices.

Asian *Lycogaster* species group together due to the armature of the female having slightly uplifted prongs on either side, and the male with two lateral subapical prongs on sternum II. However, these modifications could be derived features within *Lycogaster*, and there is otherwise not sufficient evidence to warrant dividing the Asian species from the North American species as a new genus. We have not seen the male antenna of any Asian species, but Chen (1949) described *L. violaceipennis* as lacking tyloids.

Bischoff's concept of *Lycogaster* was very broad, as he included a species with tyloids, *Lycogaster zimmeri* Bischoff, which we have transferred to *Taeniogonalos*, and a species with filiform antennae, *Lycogaster semibrunnea* Bischoff, which Riek (1954) transferred to *Taeniogonalos*.

Distribution

Lycogaster pullata is known from North America (Mexico, United States and Canada) and *L. apicipennis* is known from Central America (Mexico and Costa Rica). The other species are from eastern Asia (Indonesia, China, Burma).

Biology

North American species have been reared from Ichneumonidae parasitizing Saturniidae (Lepidoptera) (Bischoff, 1909), from Eumeninae, Vespidae (Hymenoptera) (Cooper, 1954; Parker & Bohart, 1966) and Arctiidae (Lepidoptera) (intermediate host) [LACM], (Townes, 1956). D.H. Janzen (pers. comm.) has reared *L. apicipennis* from *Enicospilus* (Ichneumonidae, Hymenoptera) parasitizing Notodontidae (Lepidoptera).

Species included

Lycogaster apicipennis (Cameron 1897). Specimens examined, COSTA RICA, 122 (EMUS, INBIO, RMNH, NHMW); MEXICO, 22 (LACM, NHMW).

Lycogaster celebesiensis (Szepligeti 1902). Type material examined: 2, **desig. lectotype n.**, to formally recognize the unpublished designation by J. Papp; INDONESIA: S. Celebes, Bua-Kraeng, 5000 ft, ii.1896 (*H. Fruhstorfer*) (HNHM). Condition, left wings broken off and glued to card (det. as 4 by Szepl.). Also examined 4, 32 from INDONESIA, CHINA (RMNH, CASC).

Lycogaster heinrichi Bischoff 1933.

Lycogaster pullata Shuckard 1841. 74 specimens from UNITED STATES, CANADA, and MEXICO: 42 EMUS, ZSMC, UMMZ, MCZC, AMNH, UCDC, CNCI and others.

Lycogaster violaceipennis Chen 1949. Examined 2 from CHINA (ZMHB).

Undetermined *Lycogaster* sp., 52 from INDONESIA, MALAYSIA, (FSAG, ANIC, USNM).

Nomadina **Westwood**

Nomadina Westwood 1868: 328. Type species *N. smithii* Westwood (by monotypy), repository: BMNH.

Liaba Cameron 1899: 3. Type species *L. balteata* Cameron 1899 (by monotypy), repository: BMNH.

Platygonalys Schulz 1905: 86. Type species *P. phylogenetica* Schulz 1905 (by monotypy), repository: ZMHB?.

Diagnosis

Length: 5.5-11 mm, FW 4.6-10.5 mm. Antennae thickened, 16-segmented; intertorulus distance about 1.2-1.9 X torulus to inner eye distance; maxillary palps rudimentary; clypeal suture below the antennal insertions; clypeus longer than wide, projecting over the base of mandibles; head relatively smooth and shiny, covered with dense short pubescence; mesosoma very smooth; FW with one closed submarginal cell (two in *N. smithii*); mesothoracic and propodeal spiracles uncovered; propodeal foramen broadly 'U' shaped, wider than tall; metasoma dorsoventrally flattened, terga and sterna very thin. Parameres rounded, 2 X wider than tall but not angled or extending past basiparamere; aedeagus expanded apically, making a 'V' perpendicular to the shaft and pointing anteriorly, shaft quite stout; female sternum II sclerotized apicomedially, armature appearing vestigial; main armature on sternum III, generally projecting over sternum IV and reaching the terminal sterna; genitalia contained in elongate flattened capsule with prominent sclerotized 'awl' pointing anteriorly.

Discussion

Nomadina is the only genus with 16 antennal segments, and may be the only genus in which the antennal segment number does not vary with size. The mesothoracic and propodeal spiracles of *Nomadina* (as well as *Bakeronymus* and *Pseudonomadina*) are uncovered while other trigonalyid genera have their mesothoracic spiracle covered by a pronotal lobe.

Nomadina and *Pseudonomadina* differ in some aspects of their male genitalia-- the basiparameres (large and stout) and parameres (reduced) are similar, but the aedeagus of the *Nomadina* is clubbed, while it is asymmetrical and knife shaped in *Pseudonomadina*. *Xanthogonalos* has parameres that are narrowly transverse, but the aedeagus is clubbed as in *Nomadina*.

Distribution

This genus is neotropical, occurring in Costa Rica, Panama, Venezuela, Ecuador, and Brazil. Although *N. balteata* is described from Chile, all known collections are from Venezuela and Ecuador. The type locality, 'Chili', is probably an error.

Biology

Nomadina have been reared from colonies of *Polybia* and *Agelaia* (Polistini, Vespidae)(BMNH). Sean O'Donnell (pers. comm.) observed *Nomadina smithii* acting as a Wasmannian mimic of small workers in a colony of *Agelaia xanthopus* (Vespidae) it was reared from.

Species included

Nomadina balteata (Cameron 1899).
=*Nomadina nasuta* Bischoff 1933. **Syn. n.**
Examined 24, 32, "Chili"?; ECUADOR, VENEZUELA (BMNH*, AEIC, IZAV).

Nomadina cisandina (Schulz 1905). Examined 72, BRAZIL (BMNH, MCZC).

Nomadina phylogenetica (Schulz 1905).

Nomadina smithii Westwood 1868. Examined 14, 32, 'Amaz.', COSTA RICA (BMNH*, CARM, UMMZ).

Pseudonomadina Yamane & Kojima

Pseudonomadina Yamane & Kojima 1982: 183. Type species _P_. _biceps_ Yamane & Kojima (by monotypy).

Diagnosis

Length 6 mm; FW in female 5.5 mm; male FW unusually short, 3.8 mm. Head wide, almost 5 X as wide as long (length measured from hind edge to front of median ocellus), rectangular when viewed from above, strongly cleft at vertex; head, including vertex and frons, smooth and shining; eye small compared to eye in _Bakeronymus_; antennae 13-14 segmented, each flagellomere conical, expanded apically; torulus adjacent to mandible, clypeus located between toruli, intertorulus distance about twice inner eye to outer torulus distance; maxillary palps rudimentary, 4-segmented, although segments sometimes indistinct; malar space long, receiving antenna; mandibles symmetrical, basal tooth wide, almost as wide as 3 remaining teeth; the hind trochantellus undivided; legs stout in male and slender in female; marginal cell slightly darkened; number of submarginal cells may be a variable character as male has incomplete 2 and 3rs-m cross veins; wings projecting past abdomen at rest in female but not in male; propodeal spiracle not covered; petiole only slightly laterally flattened; parameres (as exposed in side view) short, 0.25 X as long as wide, same width as basiparamere; basiparamere twice as long as wide; aedeagus laterally flattened, not expanded apically; female sternum II with small bifid tooth or rudimentary armature; sternum III with prominent bifid armature, projecting over inconspicuous armature on sternum IV and over terminal sternum; genitalia enclosed in capsule formed by flattened sternum VI and the tip modified into a sharp hollow awl set in sternum V.

Discussion

Pseudonomadina has the general appearance of a small bee with a greatly modified head. _Pseudonomadina_ is the only trigonalyid in which the width of the head exceeds the length of the mesosoma. The midline of the head is strongly cleft, and each side is slightly bulbous, giving it the appearance of parts of two heads joined at the center. The antenna is 14-segmented in the male and 13-segmented in the female, and the flagellomeres are conical, with each flagellomere coming from the center of the preceding. These characteristics, plus the vestigial maxillary palps, will distinguish this genus from all others. *Pseudonomadina* is similar to *Bakeronymus* and *Nomadina* in many characteristics as described above.

Biology and Distribution

This species was found in two of eight nests of *Ropalidia* (*Icarielia*) *flavobrunnea* (Polistini, Vespidae), from a total of about 100 nests examined in a study of Philippine *Ropalidia* (Yamane & Kojima, 1982). It is only known from these two rearings.

Species included

Pseudonomadina biceps Yamane & Kojima 1982. Examined paratype 4, 2, PHILIPPINES (USNM, RMNH). Holotype repository EIHU.

***Seminota* Spinola**

Seminota Spinola 1840, p.6, pl. 41. Type species *S. leprieurii* Spinola (by monotypy).

Bertonia Schrottky 1906: 349. Type species *B. nigra* Schrottky (by monotypy), repository: lost. Synonymy by Schulz (1906c).

Diagnosis

Body stout; head shining, rest of body except petiole punctate, dull; all black, except one species usually with small yellow spots on petiole; wings with black markings; length: 7 mm-15 mm; FW 6.5-12.5 mm. Genal carina meeting hypostomal carina, except genal and occipital carina absent in *S. depressa*; malar space long; vertex sharply angled behind ocelli toward top of occipital carina, or where it would be in *S. depressa*; clypeal suture indicated by indistinct line; suture between the anterior tentorial pits below antennae forming an upside down 'V' with a noticeable bump or pit, (much smaller than an ocellus) at the apex at about the level of the top of the torulus, similar bump above each antenna; antennae spindleform, 21-24 segments; toruli far apart, shortest distance between toruli 2-4 times shortest distance between inner eye margin and torulus; mandibles asymmetrical (one individual of _S_. _marginata_ in a reared series of six (BMNH) with mandibles symmetrical); propodeum with deep medial groove; tergum II about as long as following terga together. Paramere about as wide as long, dorsally squared and ventrally rounded; male sterna III & IV with transverse grooves; female with armature on sternum II.

Discussion

Seminota is a distinctive genus. The species are stout and all black, except for _S_. _depressa_ which usually has two light marks near the posterior margin of tergum I. The head is smooth and shining, although pubescent, and has a long flattened vertex which is angulate posteriorly just above the middle of the occipital carina. The antennae are strongly spindle-form. _Seminota_ is probably closest to _Lycogaster_, but can be easily distinguished by the punctate head of _Lycogaster_ which contrasts with the smooth, shiny head of _Seminota_.

The holotype of the type species, _S_. _leprieurii_, is missing the metasoma but differs from other _Seminota_ in its wing markings. The illustration and description of the holotype (Spinola, 1840) and the damaged holotype have the main characters of the genus but not the specific metasomal characters we have used. It appears allied to, and possibly the same as _S_. _marginata_.

Schulz states that _S_. _inquirenda_ is very similar to _S_. _marginata_ but smaller, with finer and more sporadic punctures, and a third submarginal cell that is decidedly shorter than the second. These characters vary intraspecifically in other Trigonalyidae and do not justify maintenance of two separate species names. Thus we are synonymizing *S. inquirenda* with *S. marginata*.

Distribution

Seminota is only known from the neotropics (Mexico, Costa Rica, Panama, Brazil, and Argentina).

Biology

Seminota species have been reared from Polistini (Vespidae) including *Apoica* (BMNH), *Mischocyttarus* (BMNH, IMLA), *Parachartergus* (CARM), *Polistes*, and *Pseudopolybia* (Weinstein & Austin, 1991).

Species included

Seminota depressa (De Geer 1773). Examined 54, 102, 1?(holotype) from BRAZIL, BOLIVIA, PERU, COSTA RICA (BMNH, IMLA, NHMW, OSUO, AMNH, ZMHB, OXUM, NHRS*).

Seminota laeviceps (Cresson 1879). Examined 24, 72, 'Mex', COSTA RICA, PANAMA (KIMS, MCZC, ANSP*).

Seminota leprieurii Spinola 1840. *Nec leprieuri* Spinola of Schulz, 1907a; Bischoff, 1938; and Weinstein & Austin, 1991. Examined 1? (metasoma missing), FRENCH GUIANA (MRSN*).

Seminota marginata (Westwood 1874).
=*Seminota inquirenda* Schulz 1907b. Holotype repository: MLUH? (**syn. n.**)
=*Seminota taschenbergi* Schulz 1906b. Holotype repository: MLUH (M. Dorn, pers. comm.).
Examined holotype *S. marginata*, 2, and 94, 232 from BRAZIL, ARGENTINA, VENEZUELA, PARAGUAY, COLOMBIA (USNM, UCDC, NHMW, CASC, MCZC, BMNH*, ANSP, IZAV, IMLA, AEIC, USNM, ZMHB, MLPA).

Seminota mexicana (Cresson 1879). Examined paratype 4 (ANSP) and 4, 72, MEXICO (EMUS, UCDC, LACM, CNCI).

Unplaced specimens: 2, possibly *S. laeviceps*:, MEXICO (ZMHB); 2, asymmetrical petiole, protruding clypeus, VENEZUELA (BMNH).

***Xanthogonalos* Schulz**

Xanthogonalos Schulz 1907a:17. Type species X. robertibuyssoni Schulz 1938 designated by Viereck (1914). Holotype repository MNHN, but loaned to Schulz and not returned according to notes of Berland (J. Casevitz-Weulersse, pers. comm.).

Diagnosis

Body elongate, smooth, with dense short erect pubescence; Length 9.4-10.2 mm, FW 9.0-9.3 mm. Head transverse in anterior view (especially in male); frons and vertex forming a flat sloping plane from the antennae to back of head; eyes with sparse pubescence; genal carina extending straight towards edge of mandibular base, sometimes obsolescent near end; no genal angle between genal carina and base of eye; prominent suture above each antenna ending in a small round bump; intertorulus distance and torulus to eye distance about equal; submarginal cell III square, about one third the length of the long, narrow submarginal cell II; propodeal foramen 'U' shaped. Parameres and aedeagus very similar to Nomadina; aedeagal shaft laterally flattened, 0.3 X width paramere; female sternum II with thin medioapical projection overlapping sterna III & IV; sternum III with small medioapical projection.

Discussion

Xanthogonalos is the only trigonalyid genus with pubescent eyes. This pubescence consists of short, erect, sparse bristles distinctly visible at magnification of X30 although some specimens may require searching for the right angle that highlights an area with hairs. Other characters are more difficult to use for diagnosis and too few specimens are available to distinguish among interspecific, sex specific, and intraspecific differences. Xanthogonalos is characterized by an elongate shape, females with strongly projecting armature on an elongate sternum II, and the males lack tyloids. In the male, sternum II is only slightly longer than sternum III. In most trigonalyids the back of the eye is even with the middle of the mandibular base, while in the South American specimens of Xanthogonalos the posterior margin of the eye is behind or parallel to the mandibular base

(Figs 31, 32). Females have a long malar space while males have a short malar space resulting from having a larger eye. All specimens are covered by short pubescence. In undescribed species #1, the pubescence is very dense and short, giving the body a plush appearance.

Xanthogonalos fits well within the Nomadinini, due to its armature and lack of tyloids. Schulz (1907a) placed the genus with *Seminota*, probably due to the angulate vertex and elongate submarginal cells, but the male genitalia is more similar to *Nomadina*, not *Seminota*.

The generic description in Schulz (1907a) appears to be of a composite of *Xanthogonalos* and *Trigonalys*. Schulz (1907a) described *Xanthogonalos* from three specimens: *Xanthogonalos robertibuyssoni*, the type species, from a single female from Mexico, and *X. severini* from two males with tyloids from "South America". We have identified two males without tyloids as representing an undescribed species of *Xanthogonalos*: they share the pubescent eyes and other characters of *Xanthogonalos*. The species *severini* does not belong to *Xanthogonalos* since presence or absence of tyloids does not vary intra-generically. *Xanthogonalos* species are superficially similar in coloration and elongate shape to the xanthic forms of the unrelated South American *Trigonalys sanctaecatharinae* (Schulz). We are synonymizing *X. severini* and *X. fasciatus* Bertoni with *T. sanctaecatharinae*.

Distribution

Neotropics.

Biology

Unknown.

Species included

Xanthogonalos robertibuyssoni Schulz 1907a. Examined 2, COSTA RICA (BMNH).
Undescribed species #1: 22, VENEZUELA, ARGENTINA (IMLA).
Undescribed species #2: 24, COLOMBIA (BMNH).

Trigonalyini Cresson 1887

Type genus: _Trigonalys_ Westwood 1835

Diagnosis

Body shape variable but never appearing slender and delicate. Antennae generally elongate and filiform; tyloids present, elongate-linear or oval to round, usually on more than 5-6 flagellomeres; genal carina reaching or ending immediately before mandibular base; propodeal foramen 'V' shaped, sharply angled at apex; metasomal plates strongly sclerotized; female armature, if present, on sternum II or III, only rarely both; male sternum II either flattened, concave, or convex, if flattened or convex may have a small bump or projection anteriorly; parameres variable but generally elongate.

Discussion

The Trigonalyini includes _Taeniogonalos_ and _Trigonalys_, and tentatively, _Ischnogonalos_. These taxa are generally stout bodied and males have tyloids, and at least in the groundplan, female metasomal armature. Though host data are very limited, none are known to parasitize aculeate wasps. _Taeniogonalos_ and _Trigonalys_ are easy to distinguish from each other by the shapes of their heads (Figs 22-23). _Ischnogonalos_ may be distinguished from them by its petiolate metasoma and thickened flagellomeres (Schulz, 1907a, 1908). Several genera, previously differentiated by variable characters, are synonymized under _Taeniogonalos_ and _Trigonalys_.

Ischnogonalos Schulz

Ischnogonalos Schulz 1907a: 12. Type species _Trigonalys_ _dubia_ Magretti (by monotypy).

Diagnosis (From Schulz, 1907a, 1908; Magretti, 1897)

Body small, 6 mm long, stature petite, with dense and coarse wrinkles, low-luster sheen except vertex which is glossy; pubescence erect; SAE slightly pyramid-shaped, not connected at midline; middle flagellomeres swollen, with linear tyloids. Male with bidentate 'armature' on second sternum.

Discussion

Schulz (1908) described the genus as having thin elongate tyloids, and from his illustration it appears typical of *Taeniogonalos*, except for the narrow petiole and swollen flagellomeres. This species is apparently only known from the holotype, which was apparently deposited in the MCSN and lost (V. Raineri, pers. comm.), and the status of this genus is unclear.

Distribution

Possibly Burma.

Biology

Unknown.

Species included

Ischnogonalos dubia (Magretti 1897).

***Taeniogonalos* Schulz**

Taeniogonalos Schulz 1906b: 212. Type species *Trigonalys maculata* Smith (by monotypy).

Labidogonalos Schulz 1906b: 207. Type species: *Trigonalys ornata* Smith (by monotypy). **Syn. n.**

Poecilogonalos Schulz 1906b: 212. Type species *Trigonalys thwaitesii* Westwood (by monotypy). **Syn. n.**

Lycogastroides Strand 1912: 129. Type species *L. gracilicornis* Strand (by monotypy). **Syn. n.**

Lycogonalos Bischoff 1913a: 155. Type species *L. flavicincta* Bischoff (by monotypy). **Syn. n.**

Nanogonalos Schulz 1906b: 211. Type species _N_. _enderleini_ De Santis 1980 (by monotypy). **Syn. n.**

Taiwanogonalos Tsuneki 1991: 35. Type species _T_. _alishana_ Tsuneki by original designation.

Diagnosis

Entire body punctate, including gena and vertex; length 4.3-13 mm, FW 3.8-11.5 mm. Genal carina ending near outside edge of mandibular base, often dividing or fading into sculpturing at the end; antenna filiform, tyloids linear and parallel-sided, with distinct edges; SAE present but reduced, forming triangular brow over each torulus, not connected to each other nor forming ledge above clypeus; frons between antennae flattened, only slightly angled in side view; intertorulus distance about same as shortest distance from torulus to eye; wings often with smoky or dark markings; metasomal plates strongly sclerotized, meeting laterally with little overlap; female sternum II expanded and often with armature that may or may not be bifid, armature usually does not extend posteriorly over more than half of sternum III, except in New Guinea and Australian species; sternum III without projection or ledge; male sternum II often flattened; parameres usually elongate.

Discussion

This genus is characterized by the parallel-sided, usually elongate tyloids, and reduced SAE that often has a light-colored mark. The intertorulus area is relatively flattened and the dorsal edge of each torulus is slightly raised: in anterior view the dorsal edge forms a 45-60° angle to the horizontal plane and in dorsal view the dorsal edge of the torulus forms a small projecting triangle (Fig. 17). The metasomal plates are always strongly sclerotized. The armature, if present, is located on the 2nd sternum, and not on the third. _Taeniogonalos flavocincta_, tentatively placed in this genus, is exceptional in that its main armature is on the third sternum with a distinct protrusion on the second. The frons is not angled either in lateral or dorsal view. The gena is punctate, as is the rest of the body in most specimens.

A number of other taxa can be confused with members of Taeniogonalos. Trigonalys maculifrons superficially resembles the sympatric Taeniogonalos ornata in shape and color pattern. The shape of the gena distinguishes the two genera (Figs 22, 23). In addition, in T. ornata the basal two-thirds of tergum I is dark brown and the remainder is yellow, the vertex and frons are evenly punctate, and a dark longitudinal line completely divides scutellum into two yellow lateral sides. In Trigonalys maculifrons the basal third or less of tergum I is dark brown and the remainder is yellow, the vertex is smooth, the frons above the antennae is textured, and the dark central line does not reach the anterior edge of the scutellum (i.e. both sides and the anterior third of the scutellum are yellow). Xanthogonalos species are also superficially similar to Taeniogonalos ornata. However, T. ornata females lack armature while Xanthogonalos females have armature on sternum II, and T. ornata males have tyloids, which are lacking in Xanthogonalos males. These species probably all mimic Agelaia species (Vespidae).

As discussed in the introduction, previous workers believed in the stability of armature as a taxonomic character and divided genera into subfamilies based in part on the presence or absence of armature. Poecilogonalos (without armature) was therefore separated from Taeniogonalos (with armature). We are synonymizing Poecilogonalos and Taeniogonalos after finding that the armature can vary not only within closely related species, but also within a species, and that the species previously separated into these two genera form part of a monophyletic group that does not warrant subdivision. Taeniogonalos thwaitesii is found from India to Malaya with closely related or the same species found in the Philippines and New Guinea. Specimens from west of Laos have a swollen sternum II but no armature, and east of Laos have sternum II with armature. Both forms are found in Laos (specimens in BPBM). Nanogonalos is also being synonymized under Taeniogonalos. Nanogonalos had been separated from Taeniogonalos by the absence of armature and an elongate body shape. However, these characteristics are insufficient to distinguish genera and *Nanogonalos* clusters with *Taeniogonalos* in the phylogenetic analysis.

Tsuneki (1991) described *Taiwanogonalos* as closely allied to *Orthogonalys*, but having tyloids. He based this relationship on the similarity of the SAE to that of *Orthogonalys*, without considering the form of the gena, genal carina, propodeal foramen, or the form of the metasomal terga. Tsuneki (1991) apparently described the seven species of his *Taiwanogonalos* from eight specimens that Teranishi had identified as *Taeniogonalos maga*. Five of these specimens, representing four species, were collected at the same time and location.

The female of *Taeniogonalos flavocincta* was previously unknown. Tentatively placed in *Taeniogonalos*, *T. flavocincta* shares the critical synapomorphies with the group: tyloids present (Teranishi, 1929), narrow, punctate genae, and typical reduced supra-antennal elevation, but is distinct because its main armature is on sternum III, with only a small projection on sternum II.

There are other sources of confusion in this group. When Schulz (1906b) described the new genus *Nanogonalos* he used a specimen from Bolivia. In the description he said he initially planned to give the specimen the species name '*enderleini*' but before publishing decided the specimen was the same as the Mexican *Trigonalys fasciatipennis* Cameron. Schulz (1906b) then described *Nanogonalos* based on the Bolivian specimen, and due to mistaken identity, Cameron's species became the type of the genus. Later, when Schulz (1907b) was able to examine Cameron's syntypes, he realized that it was not the same genus as his Bolivian specimen. Schulz's response was to call the Bolivian specimen *Nanogonalos fasciatipennis* Schulz. This decision violates article 49 of the International Code of Zoological Nomenclature, which prohibits the re-use of a species-group name wrongly applied through misidentification even if the species are later assigned to different genera. To correct Schulz's error, De Santis (1980) replaced

Nanogonalos fasciatipennis Schulz with N. enderleini Schulz. However, as enderleini was at that time a nomen nudum and unavailable De Santis (1980) becomes the author as he has given the species the replacement name. Furthermore, Taeniogonalos fasciatipennis (Cameron 1897) was described from two specimens from separate locations. Since the female is actually T. gundlachii, we are designating the male as lectotype. Females of T. fasciatipennis do not have armature, and the males have a convex sternum.

Synonymy of Lycogastroides under Taeniogonalos is based on the examination of the holotype of the type species, Lycogastroides gracilicornis Strand, and the study of paratypes of Benoit's two species in that genus, all of which are unambiguously Taeniogonalos. Benoit (1950) correctly described Lycogastroides maynei as having the armature on sternum II, but later (1951) incorrectly stated that in Lycogastroides sternum III is armed. Synonymy of the genus Lycogonalos, described from a single male specimen (Bischoff, 1913a), is based on the examination of that specimen. Although this specimen is missing the metasoma, Bischoff (1913a) described the "armature" as located anterior of a flattened area on sternum II, a feature known only from male Taeniogonalos.

We are synonymizing T. costalis under T. gundlachii. Specimens of 'T. costalis' from North and central America have less extensive yellow markings than T. gundlachii from Cuba, but specimens from Florida are intermediate. This is the only species of Taeniogonalos known in the U.S. and Canada. In the drawing of the T. gundlachii (=costalis) head in Townes (1956), the antennae are too far apart and the SAE is reduced, so that except for the distinct clypeal suture, the head resembles that of Lycogaster. Schulz (1907a) synonymized the female Trigonalys costalis Cresson with the male of the completely unrelated species Trigonalys pulchella Cresson, and placed pulchella in the genus Tapinogonalos. Bischoff (1938) removed costalis from synonymy with pulchella and placed costalis in Lycogaster. Townes (1951) moved costalis into Poecilogonalos. The presence of armature in the female and tyloids in the male places this species in

Taeniogonalos under Schulz's system as well as in the current classification. Schulz (1907a) left *Trigonalys gundlachii* as a species whose generic placement was doubtful, and Bischoff (1938) and Weinstein & Austin (1991) placed the species in *Lycogaster*. Alayo (1974), recognizing the close relation of *gundlachii* to *costalis*, followed Townes (1956) and placed the species in *Poecilogonalos*.

Distribution

Taeniogonalos, is the most widely distributed of all trigonalyid genera, and is found everywhere trigonalyids occur, except Europe and western North America. Most species are from eastern Asia and South America.

Biology

Taeniogonalos species have been reared from a variety of tachinid and ichneumonid parasitoids of Lepidoptera. *Taeniogonalos thwaitesii* has been reared from an ichneumonid parasitoid of *Lygropia quaternalis* (Pyralidae) (USNM) and from cocoons of *Henicospilus rufus* (Ichneumonidae) collected in the soil of a tea plantation (USNM, LACM) (Clausen, 1929). *Taeniogonalos gundlachii* has been reared from a tachinid, *Nilea lobeliae*, parasitizing a noctuid *Acronicta lobeliae* (Riley & Howard, 1891; Schulz, 1907a) and another tachinid, *Lespesia* sp. from a noctuid, *Phosphila turbulenta* (Carlson, 1979). It has also been reared from unidentified tachinids from *Anisota senatoria* (Saturniidae)(TAMU) and *Megalopyge opercularis* (Megalopygidae)(NCSU). A specimen from North Carolina (NCSU) has the label information that it was reared from a larva of *Apantesis anna* (Arctiidae). In Costa Rica *T. gundlachii* has been reared from both tachinid (*Lespesia*, *Blepharipa*, *Winthemia*, *Zizyphomyia*, and *Drino*) and ichneumonid (*Enicospilus* and ?*Trogus*) parasitoids of various large bodied Lepidoptera (D.H. Janzen, pers. comm.). In Kansas this species was reared from the tachinid, *Allophorocera arator*, parasitizing a detritivore tipulid, *Tipula* ?*flavoumbrosa* (Gelhaus, 1987). *Taeniogonalos maynei* was reared from pupae of *Latoia albipunctata* (Limacodidae), presumably an intermediate host (Benoit, 1950). In Australia, *Taeniogonalos maculata* and *T. venatoria* have been reared directly from pergid sawfly hosts including *Perga condiei*, *P. dorsalis*, *P. nemoralis*, and *P. affinis* (Carne, 1969; Raff, 1934; Weinstein & Austin, 1991, 1995a, b). In some cases this parasitism was apparently host density-dependent, and caused a significant reduction of the pest sawfly numbers (Carne, 1969). Riek (1962b) reared an unidentified *Taeniogonalos* from an ichneumonid parasitizing an anthelid (Lepidoptera) and a male and female *T.* ?*maculata* were reared from *Panacela lewini* (Eupterotidae, Lepidoptera)(ANIC). The report of *Taeniogonalos* directly parasitizing geometrid and tortricid cocoons (Weinstein & Austin, 1991) was not confirmed (A. Austin, pers. comm.; I.D. Naumann, pers. comm.).

Species Included

Taeniogonalos chadwicki Riek 1954.

Taeniogonalos enderleini (De Santis 1980). Transferred from *Nanogonalos*. **Comb. n.**
Examined 584, 362 from South America (AEIC, CNCI, MCZC, OSUO, NHMW, UCDC, BMNH, PORT, IMLA, CUIC, ISNB, CDFA, ZMHB*).

Taeniogonalos fasciata (Strand 1913). Transferred from *Poecilogonalos*. **Comb. n.**
=*Poecilogonalos magnifica* Teranishi 1929. **Syn. n.**
Examined 24, 182 from TAIWAN, JAPAN, CHINA, INDONESIA, MALAYSIA (AEIC, NHMW, RMNH, BMNH, CNCI, ZMUC, CARM, CMNH, TARI).

Taeniogonalos fasciatipennis (Cameron 1897). Type material examined: **desig. lectotype n.**:
2 syntype of *T. fasciatipennis* examined, = *T. gundlachii*. (BMNH). Examined: 114, 92 from MEXICO (BMNH*, CUIC, CNCI, EMUS). Same or closely related species from COSTA RICA and HONDURAS (42; USNM, FSCA, PORT, CARM).

Taeniogonalos flavicincta (Bischoff 1913a). Transferred from *Lycogonalos*. **Comb. n.**
Holotype examined, 4, no locality (ZMHB*).

Taeniogonalos flavocincta (Teranishi1929). Tentative placement, transferred from *Nanogonalos*. **Comb. n.**
Examined 4, 2, KOREA (USNM, HNHM).

Taeniogonalos formosana (Bischoff 1913a). Transferred from *Poecilogonalos*. **Comb. n.**

Taeniogonalos fulvoscutellata (Ayyar 1919). Transferred from *Poecilogonalos*. **Comb. n.**
Examined 34, 72, INDIA (USNM, RMNH, BMNH, OSUO).

Taeniogonalos gracilicornis (Strand 1912). Transferred from *Lycogastroides*. **Comb. n.**
Holotype examined, 2, EQUATORIAL GUINEA (ZMHB*).

Taeniogonalos gundlachii (Cresson 1865). Transferred from *Poecilogonalos*. **Comb. n.**
=*Trigonalys costalis* Cresson 1867. Transferred from *Poecilogonalos*. Described in *Trigonalys* and also placed in *Lycogaster*. **Syn. n.**
Numerous specimens from CANADA, COSTA RICA, CUBA, UNITED STATES (MEMU, NCSU, INBIO, TAMU, USNM, ZSMC).

Taeniogonalos henicospili (Rohwer 1929). Transferred from *Poecilogonalos*. **Comb. n.**

Taeniogonalos intermedia (Chen 1949). Transferred from *Poecilogonalos*. **Comb. n.**

Taeniogonalos javana (Bischoff 1933). Transferred from *Poecilogonalos*. **Comb. n.**
Holotype examined, 2, INDONESIA (ZMHB).

Taeniogonalos jucunda (Westwood 1868). Examined 22, 'Amazons', COLOMBIA (OXUM*, BMNH).

Taeniogonalos kerala (Ayyar 1919). Transferred from *Poecilogonalos*. **Comb. n.**

Taeniogonalos lugubris (Westwood 1868). Examined 2, 'Amazons' (OXUM*).

Taeniogonalos maculata (Smith 1851). Examined 19 specimens from Australia (ANIC).
Type repository, BMNH.

Taeniogonalos maga (Teranishi 1929). Tentative generic placement, transferred from *Poecilogonalos*. **Comb. n.**
=*Poecilogonalos yuasai* Teranishi 1938 (syn. by Tsuneki 1991).
Holotype examined, 2, JAPAN (Ibaraki*).
=*Taiwanogonalos alishana* Tsuneki 1991
Holotype examined, 2, TAIWAN (OMNH*).
=*Taiwanogonalos alticola* Tsuneki 1991
=*Taiwanogonalos claripennis* Tsuneki 1991
=*Taiwanogonalos laeviceps* Tsuneki 1991
=*Taiwanogonalos minima* Tsuneki 1991
=*Taiwanogonalos satoi* Tsuneki 1991
=*Taiwanogonalos similis* Tsuneki 1991
Examined 82 specimens from JAPAN and TAIWAN (AEIC, CNCI, TARI).

Taeniogonalos maschuna (Schulz 1907a). Tentative placement, transferred from *Tapinogonalos*. **Comb. n.**
Holotype examined, 2, missing head, ZIMBABWE (ZMHB*).

Taeniogonalos maynei (Benoit 1950). Transferred from *Lycogastroides*. **Comb. n.**
Examined 4 paratype, ZAIRE (MRAC).

Taeniogonalos ornata (Smith 1860). Transferred from *Labidogonalos*. **Comb. n.**
Examined 194, 212 from COSTA RICA and MEXICO (BMNH*, ZMHB, AEIC, UMMZ, EMUS, UCDC, TMSA).

Taeniogonalos pictifrons (Smith 1860). Described in "*Trygonalys*" [sic] and here transferred from *Lycogaster*. **Comb. n.**
Examined 22, INDONESIA [OXUM (syntype); RMNH].

Taeniogonalos raymenti **New replacement name**.
Taeniogonalos tricolor Rayment 1952

Taeniogonalos rufofasciata (Chen 1949). Transferred from *Poecilogonalos*. **Comb. n.**

Taeniogonalos sauteri Bischoff 1913a.
=*Poecilogonalos flavoscutellata* Chen 1949 (syn. by Tsuneki 1991).
=*Taeniogonalos pictipennis* Strand 1914 (syn. by Tsuneki 1991).
Examined 7 2 from PHILIPPINES, TAIWAN (AEIC, USNM, CASC).

Taeniogonalos schulzi (Bischoff 1933). Transferred from *Nanogonalos*. **Comb. n.**

Taeniogonalos semibrunnea (Bischoff 1951). Tentative identification, 34, 102 from AUSTRALIA (MAMU).

Taeniogonalos taihorina (Bischoff 1914). Transferred from *Nanogonalos*. **Comb. n.**

Taeniogonalos tenebrosa Riek 1954.

Taeniogonalos thwaitesii (Westwood 1874). Described in *Trigonalys* and here transferred from *Poecilogonalos*. **Comb. n.**
Examined 94, 302 from INDIA, SRI LANKA, THAILAND, LAOS, MALAYSIA, PAPUA NEW GUINEA, TAIWAN (BMNH, BPBM, USNM, LACM, OSUO, AEIC, OXUM*).

Taeniogonalos tricolor (Chen 1949). Transferred from *Poecilogonalos*. **Comb. n.**
Examined 62, CHINA, THAILAND, KOREA (USNM, HNHM).

Taeniogonalos venatoria Riek 1962. 215 specimens from AUSTRALIA (ANIC, AEIC).

Taeniogonalos zairensis (Benoit 1950). Transferred from *Lycogastroides*. **Comb. n.**
Examined 2 paratype, ZAIRE (MRAC).

Taeniogonalos zimmeri (Bischoff 1933). Transferred from *Lycogaster* based on male having tyloids (Bischoff 1933). **Comb. n.**

Unplaced specimens: *Taeniogonalos* sp. 1: ARGENTINA, 24, 2, (IMLA, AEIC). *Taeniogonalos* sp. 2: 4, PAPUA NEW GUINEA (UCDC). *Taeniogonalos* sp. 3: 2, INDONESIA (RMNH). *Taeniogonalos* sp. 4: 214, 162, PAPUA NEW GUINEA (ANIC).

Trigonalys **Westwood**

Trigonalys Westwood 1835: 52. Type species *T. melanoleuca* Westwood (by monotypy).

Trigonalos Schulz 1906a, emended without justification; *Trigonalis* Spinola 1840, incorrect subsequent spelling.

Stygnogonalos Schulz 1907b:305. Type species *Trigonalys* *championi* Cameron (by monotypy). **Syn. n**.

Discenea Enderlein 1905: 200. Type species *Trigonalys* *natalensis* Kreichbaumer (by monotypy). **Syn. n**.

Lycogastrula Strand 1912: 130. Type species *L*. *micanticeps* Strand (by monotypy).

Stygnogonaloides Strand 1912: 128. Type species *S*. *crassiceps* Strand (by monotypy).

Diagnosis

Length 6.2-13 mm, commonly 8-10 mm, FW 4.9-10.6 mm. Occiput strongly excavated all the way to mandibular base; genal carina extending straight and unbranched to lateral edge of mandibular base without getting smaller; genal carina on genal angle (Fig. 22), area around the end of carina smooth, not rough; gena wide in side view and shining behind lower part of eye; malar space short; antennae elongate and filiform; tyloids small, rounded and often glistening; intertorulus distance about equal or a little less than distance from torulus to inner margin of eye; lower face above clypeal suture and area between antennae not punctate, usually shining; frons sharply angled in side view, with slight carina between antennae; female armature present or absent, if present generally on sternum III, rarely on II or II & III; female tergum V often hoodlike, with flange over posterior segments; male metasoma rounded ventrally.

Discussion

Members of this genus are the only trigonalyids that have the genal carina located on the genal angle, and have the occiput strongly excavated all the way to the mandibular base (Fig. 22). The SAE join together forming a ledge between the base of the antennae and the area between the ledge and the clypeal suture is shiny, as is the gena.

A number of *Trigonalys* species resemble those of other genera. *Trigonalys* *flavescens*, with its smooth metasoma, orange color and elongate shape, superficially resembles _Orthogonalys_. However, in _T. flavescens_ the genal carina ends at the mandible base while in _Orthogonalys_ the genal carina fades before reaching the hypostomal carina, and in _Trigonalys_ the head is more hemispherical. _Trigonalys maculifrons_ can be separated from the superficially similar _Taeniogonalos ornata_ by the generic differences in head shape and the slight differences in color patterns described in the discussion of _Taeniogonalos_, the key to New World genera, and figures 22 and 23.

We are synonymizing _Discenea_ and _Lycogastrula_ with _Trigonalys_. These genera were erected for species known only from Africa, but these species share the generic characteristics of _Trigonalys_. Bischoff (1951) argued for the synonymy of _Lycogastrula_ within _Discenea_ while Benoit (1950, 1951) placed _Lycogastrula_ in the subfamily Lycogastrinae and erected the subfamily Disceneinae. Weinstein & Austin (1991) recognized Benoit's subfamily Disceneinae but not Benoit's acceptance of the genus _Lycogastrula_.

Trigonalys melanoleuca is represented by two syntypes [BMNH, OXUM]. We are designating the BMNH specimen, a female, as lectotype. The wings of the lectotype are spread and it is missing the left hind leg, both middle legs, and the tips of both antennae.

Sharp (1895) illustrated _Trigonalys maculifrons_ with the caption "_Trigonalys maculifrons_ Cam. _i.l_. Mexico." prior to Cameron's (1897) description of the species. Since the illustration clearly depicts the holotype specimen described in Cameron (1897), Sharp is therefore the legitimate author of this species rather than Cameron.

We have seen three undescribed species allied to _Trigonalys championi_ Cameron represented by four specimens (CNCI, BMNH, EMUS, PAGL). The similar looking _Trigonalys melanoleuca_ has tergum I with the apex rounded (Fig. 37) and the female without armature. _Trigonalys championi_ has tergum I with the apex nearly straight across (Fig. 38) and the female with armature on sternum III. Additional variation within the genus can be seen comparing Figs 39-40.

The figure in Schulz's monograph (1907a) labeled *Labidogonalos ornata* is actually *Trigonalys sanctaecatharinae* from South America. In *T. sanctaecatharinae*, some females have one to three extremely reduced tyloid-like structures, instead of the normal 4-8 tyloids per antenna found in males.

Distribution

Trigonalys is known from South and Central America, subsaharan Africa, and Asia (India and Philippines).

Biology

Although *T. melanoleuca* is one of the most commonly collected trigonalyids, its host is unknown. *Trigonalys natalensis* has been reared from an unidentified lepidopteran pupa (Schulz, 1910) and *T.* ?*micanticeps* has been recorded from a larva of *Achaea catacoloides* (Noctuidae) (BMNH).

Species included

Trigonalys championi Cameron 1897. Restored from *Stygnogonalos*. **Comb. revived.** Examined 22, GUATEMALA, COSTA RICA (BMNH*, USNM).

Trigonalys crassiceps (Strand 1912). Transferred from *Discenea*. **Comb. n.** Examined 2, EQUATORIAL GUINEA (ZMHB*).

Trigonalys flavescens (Bischoff 1951). Transferred from *Labidogonalos*. **Comb. n.** Examined 34, MEXICO (BMNH*, EMUS, PORT).

Trigonalys lachrymosa Westwood 1874. Restored from *Lycogaster*. **Comb. revived.** Examined 2, PHILIPPINES (USNM).

Trigonalys maculifrons Sharp 1895. Restored from *Labidogonalos*. **Comb. revived.** Examined 54, 192, MEXICO, COSTA RICA, HONDURAS, GUATEMALA (BMNH*, AMNH, ANSP, LACM, EMUS, MCZC, FSCA, UCDC, USNM).

Trigonalys melanoleuca Westwood 1835. Type material examined: **Desig. lectotype n.**: 2, BRAZIL (BMNH). Condition: missing very tip of both antennae, wings spread, missing left hind and middle legs. 12 paralectotype, no collection data (OXUM). Also examined 183 specimens from South America including ARGENTINA, BOLIVIA, BRAZIL, ECUADOR, GUYANA, PARAGUAY, PERU, TRINIDAD, VENEZUELA (MCZC, IMLA, BMNH, FSCA, AEIC, CNCI, UCDC, CDFA, and others).

Trigonalys micanticeps (Strand 1912). Transferred from *Discenea*. **Comb. n.**

Examined, tentative identification, 64, 132 from CAMEROON, GHANA, IVORY COAST, GABON, ZAIRE, ANGOLA (BMNH, FSAG, MRAC, CNCI).

Trigonalys natalensis Kreichbaumer 1894. Restored from *Discenea*. **Comb. revived.** Examined 24, 102 from SOUTH AFRICA, MADAGASCAR, KENYA, ZIMBABWE, ANGOLA (AEIC, BMNH, ZMHB, CNCI, UCDC, MRAC).

Trigonalys rufiventris Magretti 1897. Restored from *Lycogaster*. **Comb. revived.** Holotype not found in MCSN (V. Raineri, pers. comm.). Examined 4, 22, INDIA (MCZC, OSUO).

Trigonalys sanctaecatharinae (Schulz 1907a). Transferred from *Labidogonalos*. **Comb. n.**
=*Xanthogonalos fasciatus* Bertoni 1912, **Syn. n.**
Xanthic form of *T. sanctaecatharinae*.
=*Xanthogonalos severini* Schulz 1907a, **Syn. n.**
Examined *X. fasciatus* paratype 2, PARAGUAY (USNM). Also examined 814, 252, 9? from BRAZIL, ARGENTINA, PARAGUAY (MCZC, CNCI, AEIC, UCDC, OSUC, BMNH and others).

Genera not assigned to Tribes (within Trigonalyinae)

***Jezonogonalos* Tsuneki**

Jezonogonalos Tsuneki 1991: 32. Type species *J*. *marujamae* Tsuneki (by monotypy), repository: OMNH. Described from a single female (not male) without antennae. Tentative placement.

Diagnosis (From Tsuneki, 1991)

Head from above with SAE strongly produced anteriorly, at least as long as wide at base; SAE directly rising from frons (not from indentation); gaster robust, slightly less than twice as long as wide, forewing weakly fasciated.

Discussion

Tsuneki (1991) distinguished *Jezonogonalos* from *Taeniogonalos* *maga* by the slightly more anteriorly produced SAE. The single specimen on which the genus is based is inadequate, and more specimens in better condition are needed to evaluate its generic status.

Distribution

The specimen described by Tsuneki (1991) is from Japan.

Biology

Unknown.

Species *included*

Jezonogonalos *marujamae* Tsuneki 1991
J. *marujamanae* Tsuneki 1991 (variant spelling in original work, *J*. *marujamae* chosen by Tsuneki (1992).
Examined 2 from JAPAN (OMNH*).

***Mimelogonalos* Schulz**

Mimelogonalos Schulz 1907a: 8. Type species *M*. *bouvieri* Schulz (by monotypy).

Diagnosis

Body punctate and shiny black, with yellow clypeus and parts of legs, sometimes spots on the scutellum, dorsellum, and metasoma; length 5-9 mm, forewing 4.2-7.9 mm. Genal carina meeting mandibular base; malar space long; antennae with 22-25 segments, almost as long as body; tyloids broad and elongate, with a dull lead-like luster, surface keel shaped; toruli close together: shortest distance between toruli 0.6-0.9 times less than the shortest distance between the inner eye margin and the torulus; wings hyaline or yellowed but without dark markings; mesosoma and metasoma compact, not elongate; tergum II about as long as following terga together; parameres are truncate apically; aedeagus rectangular, in side view broader and more squared at the tip than in any other known trigonalyid. Female without armature, terminal sternum modified into cylindrical tube that often points straight down out of metasoma.

Discussion

This genus can be recognized by its black body with yellow markings, and shiny metasoma without ventral modifications. *Taeniogonalos*, the only other genus in Australia, has a dull-colored and punctate integument, and males have flattened metasomal sterna while females have armature. *Taeniogonalos* is often reported as black with lighter markings (Chen, 1949; Riek, 1954; Teranishi, 1929; Townes, 1956) but the 'black' is actually fuscous. In *Mimelogonalos* the metasoma is either all black or black with two dorsolateral yellow spots, while in *Taeniogonalos* the metasoma is usually transversely striped.

The holotype of *Mimelogonalos bouvieri* Schulz 1907a was reported as lost and the species redescribed by Riek (1954) but a neotype not designated (article 75, International Code of Zoological Nomenclature). Berland recorded that the holotype was loaned to Schulz and not returned (J. Casevitz-Weulersse, pers. comm.).

Mimelogonalos contained only *M. bouvieri* until Rayment (1952) described a second species, and Riek (1954) added four others. All six appear closely related. Riek (1954) separated species using characters including the number of antennal segments and the extent of color markings. These characters vary within a single species in other genera. Since Riek based his species on one or two specimens, and since he was only able to examine two specimens of *M. bouvieri*, he was unable to assess the extent to which the species varied. Thus, many specimens now available do not fit his key. Based on our study of Riek's *Mimelogonalos* type material, we have synonymized *M. punctulata* and *M. partiglabra* under *M. bouvieri*. Additional specimens of this rarely collected genus are required to evaluate the status of the remaining species.

Two undescribed females (ANIC, ZMHB) of the smallest trigonalyids we have seen may belong to *Mimelogonalos*. They are from Australia and are about 3 mm long (forewing 2.7 mm). These differ from other *Mimelogonalos* in that the genal carina ends inside of the mandibular base instead of bending at the end toward the mandibular base, and their mandibles are symmetrical. These differences could be due to their small size. More specimens, especially males, are needed before their relationships can be confirmed.

Distribution

Mimelogonalos species are known only from eastern Australia including Tasmania.

Biology

Unknown.

Species included

Mimelogonalos bouvieri Schulz 1907a.
=*Mimelogonalos partiglabra* Riek 1954 (**syn. n.**).
=*Mimelogonalos punctulata* Riek 1954 (**syn. n.**).
Examined holotype *M. punctulata*, 2 (ANIC); holotype *M. partiglabra*, 2 (ANIC) and 104, 112, all from AUSTRALIA (ANIC, AEIC).

Mimelogonalos minuta (Rayment 1952). Examined 4, 72, AUSTRALIA (ANIC, BPBM).

Mimelogonalos nigricauda Riek 1954. Examined 4, AUSTRALIA (ANIC*).

Mimelogonalos nigrithorax Riek 1954. Examined 2, AUSTRALIA (ANIC*).

Undescribed, small species, from Australia, tentatively placed, 22 (ANIC).

***Pseudogonalos* Schulz**

Pseudogonalos Schulz 1906b: 209. Type species *Trigonalis* [sic] *hahnii* Spinola (by monotypy), repository: MRSN (Scaramozzino & Pagliano, 1989).

Diagnosis

Body slender, elongate, shiny black; metasoma and head sparsely punctate, mesosoma punctate to rugose; length 5.5-13.9 mm, FW 4.3-9.4 mm. Genal carina meeting hypostomal carina with occiput deeply excavated; malar space short; SAE large vertical ligulate lobes whose upper and mesal parts are rounded, smooth and shiny while lower and distal portions form the torulus; antennae very close together: shortest distance between toruli 0.4-0.7 X the shortest distance between inner eye margin and torulus; tyloids present, round to slightly ovoid; terga slightly overlapping sterna (not meeting laterally); tergum II longer than tergum III but not as long as all the following terga together; paramere as wide as basiparamere and 1.4 times as long as wide; basiparamere slightly longer (1.3X) than paramere; aedeagus similar to *Orthogonalys*, cylindrical with a capitate tip; female terminalia without armature and sternum not expanded; terminal sternum in female pointing backwards, not strongly sclerotized or sharply pointed.

Discussion

The SAE in the shape of a thin anteriorly projecting lobe mesad of the torulus and the fasciate forewing are diagnostic for this genus. The genal carina ending at the hypostomal carina, with the occiput deeply excavated at the genal carina posteriorly but flattened near the hypostomal carina are also distinctive features. The relationships of the genus are obscure: the tyloids are closest in shape to *Trigonalys*, but that genus has the SAE meeting at the midline and the genal carina going straight to the mandibular base. The terga are thickened and do not wrap around ventrally as is characteristic of *Orthogonalys*.

Oehlke (1983) recognized the name *Trigonalis* Spinola 1840 as a generic name distinct from *Trigonalys* Westwood 1835, making *Pseudogonalos* a junior synonym of *Trigonalis*. Scaramozzino & Pagliano (1989) pointed out that *Trigonalis* was a misspelling of *Trigonalys*. Spinola (1840) attributed *Trigonalis* to Klug, indicating his intent was not to describe a new genus, and later noted his error (Spinola, 1841). *Trigonalis* is an "incorrect subsequent spelling" (International Commission on Zoological Nomenclature, 1985, article 33 section c) and is not an available name. Thus the name *Pseudogonalos* stands.

Distribution

Pseudogonalos hahnii is known from Europe and parts of Asia including Siberia. Reports of this species from Japan are actually of the genus *Teranishia* (Tsuneki, 1991). *Pseudogonalos harmandi* was known from a single specimen from Darjeeling, northeastern India (Schulz, 1907a), now apparently lost.

Biology

Pseudogonalos hahnii lays eggs on the exterior of foliage (Bischoff, 1936b) and has been reared from *Diprion similis* (Diprionidae) (CNCI), and ichneumonids parasitizing Lepidoptera (Bischoff, 1938). Other host records are unconfirmed. Reports that *P. hahnii* parasitizes yellowjackets (or their parasitoids) (Clausen, 1940; Thompson, 1958; Weinstein & Austin, 1991) apparently started with speculation of Dours (1873) that was never confirmed (Bischoff, 1936a, b; Reichert, 1911). The reports (Rayment, 1948; Weinstein & Austin, 1991) of this palearctic species as a parasitoid of the neotropical *Polistes lanio* are clearly improbable and stem from a misreading of Sharp (1895). Again, through a misreading of the original text, Weinstein & Austin's (1991) citation of Popov (1945) reporting that *P. harmandi* parasitizes ichneumonids is erroneous.

Species included

Pseudogonalos hahnii (Spinola 1840). Examined ca. 90 specimens from Europe and Asia Minor (ZSMC, MNHN, CNCI, FSAG, TMSA, CASC, NHMW, PAGL).

Pseudogonalos harmandi Schulz 1907a.

Teranishia **Tsuneki**

Teranishia Tsuneki 1991: 15. Type species *T. nipponica* Tsuneki (by monotypy), repository: OMNH.

Diagnosis

Body slender, elongate, head and metasoma shiny black, thorax deeply punctate; metasoma fusiform; length 8 mm [10-12 mm (Tsuneki, 1991)] FW 6.8 mm. Genal carina ending before hypostomal carina; gena shiny with sparse long white pubescence emerging from punctures; malar space narrower than or approximately equaling width of first flagellomere; antennae long, filiform, with 25 [24-27 (Tsuneki, 1991)] segments, not banded; toruli closer together than shortest distance between torulus and inner eye margin; SAE strongly lobed and pointing anteriorly, dorsal margin slightly indented; FW lightly fasciated behind stigma, darkest anteriorly at either side of 2r-rs; submarginal cell 2 rarely petiolate; propodeal foramen 'V' shaped with a 'U' shaped carina around it (similar to *Pseudogonalos*); terga thin, wrapping laterally but not ventrally; tergum II slightly longer than III; terminal female sternum tightly folded and pointing posteriorly, not strongly sclerotized or awl-like.

Discussion

According to Tsuneki (1991), who described *Teranishia* from a series of 9 males and 7 females, this genus has a lobed SAE on the frons similar to *Pseudogonalos* but lacks tyloids. We have not seen males in this genus but the females do appear very close to *Pseudogonalos hahnii*. Females in the genus *Teranishia* Tsuneki appear to share many primitive traits with *Orthogonalys*, but more importantly, share derived character states with *Pseudogonalos*. As males of *Teranishia* were not available for this study we were only able to tentatively evaluate the phylogenetic position of this genus.

Distribution

The specimens described by Tsuneki (1991) is from Japan.

Biology

Unknown.

Species included

Teranishia nipponica Tsuneki 1991. Examined 22 from JAPAN (AEIC, CNCI).

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