

# The systematics and biology of the Costa Rican species of parasitic wasps in the *Thyreodon* genus-group (Hymenoptera: Ichneumonidae)

IAN D. GAULD<sup>1</sup>\* FLS and DANIEL H. JANZEN<sup>2</sup>

<sup>1</sup>The Natural History Museum, Cromwell Road, London SW7 5BD, UK

<sup>2</sup>Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

Received June 2003; accepted for publication November 2003

This paper presents an eco-taxonomic study of the Neotropical representatives of the *Thyreodon* genus-group (Hymenoptera: Ichneumonidae) present in Costa Rica, i.e. species of the genera *Thyreodon* and *Rhynchophion*. These ichneumonids are koinobiont endoparasitoids of the larvae of Sphingidae and Saturniidae. Intensive sampling in Costa Rica, conducted over 15 years, has revealed the presence of 23 species (12 of which are described here as new – *Rhynchophion woodi*, *Thyreodon woodleyi*, *T. papei*, *T. whitfieldi*, *T. deansi*, *T. walkerae*, *T. sharkeyi*, *T. zitaniae*, *T. delvarei*, *T. schauffi*, *T. darlingi* and *T. carmeani*), whereas earlier studies recognized only nine species in the same area. Several of the additional species we found are simply very scarce and thus unlikely to be encountered except by the type of intensive survey that, in the tropics, has only been conducted in Costa Rica. In some other cases, it has become apparent that more than one species has previously been confused under a single name. *Thyreodon rufothorax* Cameron is shown to be morphologically and biologically distinct from *T. atriventris* (Cresson), with which it has long been synonymized, and the relatively well-known, chromatically distinctive species '*T. laticinctus* Cresson' and '*T. morosus* Smith' are both shown to be complexes of sibling species. Reared series have been essential in facilitating the separation of the species in these complexes. An illustrated key is provided to separate all taxa using simple morphological characters. Fourteen of the 23 species have been reared, and all have been found to be restricted to one or a few species of hosts, species of *Thyreodon* primarily on macroglossine Sphingidae (with one species on Saturniidae) and species of *Rhynchophion* on sphingine sphingids of the genus *Manduca*. No two species of these ichneumonids attack the same host caterpillar species, and not all species of macroglossines present in the study area are attacked by species in this genus-group. Most species are apparently rather rare. Many have only been collected by rearing on a few occasions, other species have been collected at light (six in total) or in Malaise traps (ten in total), or by hand-netting (20 in total), but no one method collected all of the species present in the principal study area, the Area Conservacion de Guanacaste. The two New World genera *Rhynchophion* and *Thyreodon* are found to be related to the Old World genera *Dictyonotus* and *Euryophion*, the former of which comprises species that are also sphingid parasitoids, whereas species of the latter attack the caterpillars of other large bombycoid moths, Saturniidae and Eupterotidae. A cladistic analysis shows that *Thyreodon* is the sister-lineage to *Dictyonotus*, and *Euryophion* is the most basal lineage in the genus-group. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 141, 297–351.

ADDITIONAL KEYWORDS: Area de Conservacion Guanacaste – biodiversity – caterpillar – inventory – parasitoid – Saturniidae – Sphingidae.

## INTRODUCTION

Although many very species-rich groups of Ichneumonidae parasitize immature Lepidoptera, rather few attack sphingid caterpillars (Janzen & Gauld, 1997).

Several of those that do, *Cryptophion* in the Campopleginae and the *Callajoppa* complex of Ichneumoninae, have recently been the subject of detailed taxonomic, phylogenetic and biological study (Gauld & Janzen, 1994; Sime & Wahl, 2002). Here we examine the systematics and natural history of the Mesoamerican species of the third major and only other sphingid-parasitizing ichneumonid lineage, the *Thyreodon*

\*Corresponding author. E-mail: I.Gauld@nhm.ac.uk

genus-group. This genus-group is a clade of the Ophioninae that comprises four genera, *Dictyonotus* Kriechbaumer, *Euryophion* Cameron, *Rhynchophion* Enderlein and *Thyreodon* Brullé (Cushman, 1947; Gauld, 1985). A little-known southern Palaearctic genus, *Barytatocephalus* Schluz, should perhaps be included as the very basal member of this group (Gauld, 1985), but because nothing is known of its biology and very few specimens have been collected, it is not discussed further here.

This study focuses on the 23 species present in Costa Rica because this is the only tropical American country that has been intensively sampled for Ichneumonidae, and because there is a large and growing body of information about the natural history of Costa Rican species. In Costa Rica, members of the *Thyreodon* genus-group occur in all habitats from dry forest to rain forest to the lower margins of cloud forest (from sea-level to about 1400 m), but appear to be most abundant as adults and as rearing records in dry forest, and where dry forest intergrades with rain forest and cloud forest.

Unfortunately, most species of the *Thyreodon* genus-group are very rarely collected by general collecting. Very few (except for *Rhynchophion flammipennis*) are ever taken in Malaise traps, even when the trapping has been extremely intensive and the species is known to occur in the surrounding forest. For example, in the dry forest of Sector Santa Rosa of the Area de Conservacion Guanacaste (ACG) in north-western Costa Rica (<http://www.acguanacaste.ac.cr>), no specimens of *Thyreodon santarosae* have ever been Malaise-trapped in 36 trap years of sampling, although numerous individuals have been reared from caterpillars collected in the forest canopy immediately above and even adjacent to the Malaise traps. Likewise, 13 other Costa Rican species have never been found in Malaise trap samples despite hundreds of Malaise trap years throughout the country by INBio and by the Universidad de Costa Rica (Table 1). Light traps yield reasonable numbers of a rather few species (such as *T. atriventris* and *T. rivinae*), but many others have only been rarely collected, either by net (such as *T. papei*, *T. deansi* and *T. schauffi*) or by rearing. A large proportion of the specimens reported on here have been reared. Of the 23 Costa Rican species, two (*R. woodi*, *T. woodleyi*) are still known only from reared material. Currently we know the hosts of more species from the ACG than are known for the remainder of the entire Neotropical region, largely because of the intensive biodiversity inventory of caterpillars, their food plants and their parasitoids in the 110 000 terrestrial hectares of the ACG (e.g. Janzen & Gauld, 1997; Burns & Janzen, 2001; Schauff & Janzen, 2001; Janzen, 2003; Janzen *et al.*, 2003).

**Table 1.** The collecting method employed for sampling in Costa Rica since about 1980, and the species yielded by a particular method (+) or never collected by the method (–) despite fairly intensive use of at least the first three methods throughout the Costa Rican National park system. Rearing has only been undertaken in the ACG, and species not known to occur within this area are denoted by an asterisk (\*)

Species	mv light	Malaise	hand net	reared
<i>R. flammipennis</i>	–	+	+	+
<i>R. woodi</i>	–	–	–	+
<i>T. woodleyi</i>	–	–	–	+
<i>T. papei</i>	–	–	+	–
<i>T. santarosae</i>	+	–	+	+
<i>T. niger*</i>	–	–	+	–
<i>T. morosus</i>	–	+	+	–
<i>T. laticinctus</i>	–	+	+	+
<i>T. whitfieldi</i>	–	+	+	+
<i>T. deansi</i>	–	–	+	–
<i>T. apricus</i>	–	+	+	+
<i>T. walkerae</i>	–	–	+	+
<i>T. erythrocerata</i>	–	–	+	+
<i>T. sharkeyi</i>	–	–	+	+
<i>T. zitaniae</i>	–	+	+	–
<i>T. delvarei</i>	–	+	+	–
<i>T. schauffi</i>	–	–	+	+
<i>T. rivinae</i>	+	–	+	–
<i>T. maculipennis</i>	+	–	+	+
<i>T. darlingi</i>	–	+	+	–
<i>T. carmeani*</i>	+	–	–	–
<i>T. rufothorax</i>	+	+	+	+
<i>T. atriventris</i>	+	+	+	+

It is noteworthy that Gauld (1988) recorded just nine species of *Thyreodon* from Costa Rica by 1987, following several centuries of miscellaneous collecting by the taxonomic community. By the end of 2002, following 14 more years of intense collecting and rearing from hosts, we recognized 21. Intensive sampling found additional species and has shown that several of what were thought to be ‘the more common species’ are complexes of sibling species, separated by host caterpillars as well as morphology. It is impossible to delineate species clearly unless many specimens are available for study (although once species are delineated, identifications of single specimens are possible). The collections of tropical South American specimens are simply not sufficiently abundant nor geographically representative to do this at present. Consequently, the geographical and taxonomic status of several neotropical species that have been recorded as being widespread (e.g. by Townes & Townes, 1966) needs to be reassessed elsewhere in the light of our discovery of sibling species complexes in Costa Rica.

For example, what is generally curated as the very widespread '*Thyreodon atriventris*' in all museums is apparently at least three species.

Species of the *Thyreodon* genus-group are solitary koinobiont endoparasitoids. Oviposition may be into second through terminal (5th) caterpillar instars, but the wasp larva does not begin to consume the caterpillar until the caterpillar is prepupal and has made its pupation chamber in the soil or litter. Wasp larval development lasts 4–10 days. The final instar wasp larva emerges from the caterpillar cadaver and spins an extremely hard and tough distinctively shaped (see Fig. 67) silk and glue cocoon in the caterpillar's pupation chamber. The walls of this chamber are required as support points for the initial construction of the framework of the cocoon. The wasp larva or pupa uses either 1–2 months for development or many months (and thereby passes the inimical dry season or other caterpillar-free season).

*Thyreodon* species share their host species with a number of other species of parasitoids in the Tachinidae, Ichneumonidae, Eulophidae and Braconidae (Janzen *et al.*, 2003; Janzen & Hallwachs, 2003), but nothing is known about competitive interactions that occur among these insects. *Thyreodon* species have almost no hyperparasites, although we found two ACG species to be rarely attacked by a species of mesochorine ichneumonid, *Cidaphus rostratus* Dasch. *Thyreodon atricolor*, a north-eastern USA sphingid parasitoid, is attacked by the encyrtid, *Epiencyrtus thyreodontis* (Hooker, 1912), and a very similar species of *Epiencyrtus* has been reared from *Enicospilus lephogagus* Gauld (Ophioninae, Ichneumonidae) in the same Santa Rosa forest as the *Thyreodon* species recorded here (Janzen & Hallwachs, 2003). All natural history observations reported here are from the Janzen & Hallwachs (2003) caterpillar and parasitoid inventory of the ACG (Janzen, 2002, 2003; <http://janzen.sas.upenn.edu>). This inventory has, by the end of 2002, reared 21 000+ and 18 000+ wild-caught Sphingidae and Saturniidae, respectively, to produce the parasitoids recorded here (no neotropical member of the *Thyreodon* genus-group has ever been reared from any other caterpillar family).

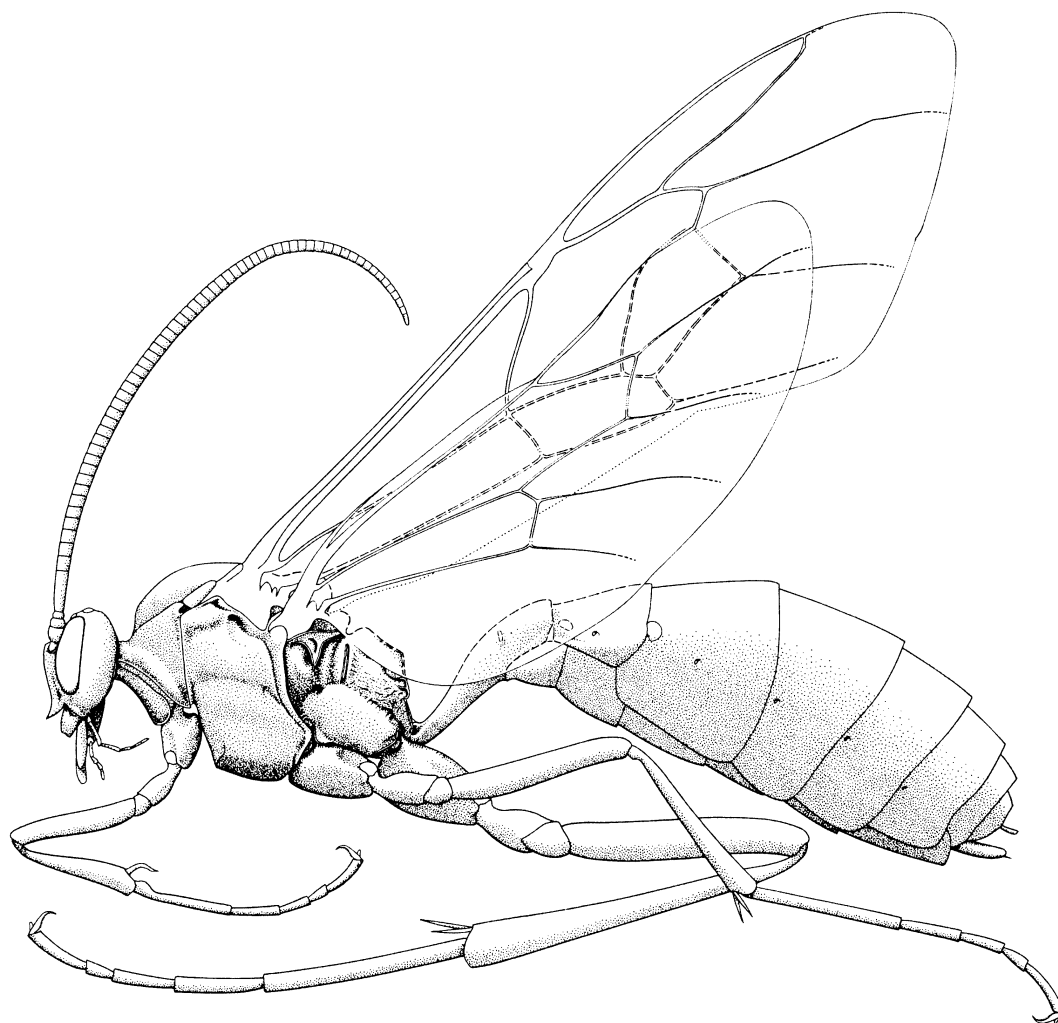
In Central America, members of the *Thyreodon* genus-group can be separated from all other ichneumonids by the combination of their large size (fore wing length 15 mm+), the laterally compressed metasoma, weakly curved and densely pectinate claws, and the absence of vein *2rs-m* in the fore wing, with *3rs-m* far distal to *2m-cu*. They differ from other large ophionines (such as *Enicospilus*, which are primarily yellowish brown with hyaline wings, see Gauld, 1988) in having black or patterned wings, and often being extensively black and metallic coloured (Figs 3–6). Unlike most other ophionines, which are predomi-

nantly nocturnally active, many species of the *Thyreodon* genus-group search for their hosts both diurnally and nocturnally. Given that the females of these strong and tough wasps can inflict a painful 'sting' with the ovipositor to the human finger, their black, yellow and/or red colours, vividly displayed during their unadroit flight, should be viewed as the result of selection associated with Batesian and Müllerian mimicry rings that also contain large black aculeate wasps (e.g. Pompilidae, Vespidae) and presumably noxious and brightly coloured diurnal Arctiidae. Our study has found all species of the *Thyreodon* genus-group to be very narrowly host-specific and low-frequency parasitoids of large naked sphingid (and in one case saturniid) caterpillars (Table 2 and Porter, 1986, 1989; Gauld, 1988). There is no case of more than one species of the *Thyreodon* genus-group using the same species of caterpillar despite as many as ten wasp species occurring in the same ACG forest (Table 2) and almost 200 potential host species.

#### TERMINOLOGY AND MATERIAL EXAMINED

Terminology throughout this work follows that used by Hanson & Gauld (1995). Depositories of specimens have been abbreviated as follows: AEIC: American Entomological Institute, Gainesville, Florida, USA; BMNH: The Natural History Museum, London, UK; CAS: California Academy of Sciences, San Francisco, California, USA; FSCA: Florida State Collection of Arthropods, Gainesville, Florida, USA; INBio: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; JHVC: Janzen and Hallwachs voucher collection. Whilst taxonomic work is underway this collection is on long-term loan to the BMNH. Such specimens are identified with the voucher alphanumeric code xx-SRNP-yyyy and their data can be obtained from <http://janzen.sas.upenn.edu>; MNHM: Museum National d'Histoire Naturelle, Paris, France; PANS: Philadelphia Academy of Sciences, Philadelphia, Pennsylvania, USA; TM: Természettudományi Múzeum Allatara, Budapest, Hungary; UCRC: Universidad de Costa Rica, San Pedro, Costa Rica; USNM: National Museum of Natural History, Washington DC, USA; ZISP: Zoological Institute, St Petersburg, Russian Federation.

Many INBio labels refer to Santa Rosa National Park and to Guanacaste National Park. The portion of the former in which collections were actually made has become Sector Santa Rosa of the Area Conservación Guanacaste (ACG), and the latter has become Sector Poco Sol, Sector Orosi and Sector El Hacha of the ACG. The portion of Rincon de la Vieja National Park in which most collections have been made is now Sector Pailas of the ACG. When localities are printed on labels on specimens, we have elected to cite them as



**Figure 1.** Whole insect, lateral. *Rhynchophion flammipennis*. Illustration reproduced with the kind permission of the American Entomological Institute.

they are, but localities for reared vouchers are given by their current microgeographical locations within the ACG, available at <http://janzen.sas.upenn.edu>.

I. D. Gauld is the sole author of all the species described here. The whole insect line drawings (Figs 1, 2) are based on specimens in the AEIC (labelled as such) and are the same as used in Townes (1971). Photographs are from specimens in BMNH and JHVC and labelled accordingly.

#### THE GENUS *RHYNCHOPHION* ENDERLEIN

*Rhynchophion* Enderlein, 1912: 630. Type species: *Rhynchophion odontandropax* Enderlein, by original designation.

**Diagnosis:** Large, stout insects, fore wing length 18.0–29.0 mm, black or red-brown in colour with blackish or mottled wings. Head in anterior view with labio-

maxillary complex elongate, projecting ventrally by about 0.5 of length of head; maxillary palpi slender; clypeus with margin out-flared, thin, centrally with an obtuse point; ocelli small, the lateral ones separated from eye by more than their own diameter; occipital carina complete dorsally, ventrally not reaching hypostomal carina. Antenna short and stout, setaceous, the central flagellomeres transverse. Pronotum unspecialized; notauli obsolescent; lateral part of metanotum swollen and carinate; propodeum convex, but not greatly inflated, posteriorly mediodorsally without a median longitudinal furrow. Hind coxa moderately large, its apex projecting beyond hind margin of propodeum. Fore wing with abscissa of *1m-cu* distal to bulla slightly shorter than abscissa of *M* between *2m-cu* and *3rs-m*. Metasoma with tergite II small, very conspicuously shorter than tergite III; male with dorsal margin of clasper notched; aedeagus with a sharp subapical lateral keel; male subgenital plate strongly



KEY TO SPECIES OF THE *THYREODON* GENUS-GROUP PRESENT IN COSTA RICA

1. Head, in anterior view, with labiomaxillary complex elongate, projecting well below labrum, and with maxillary palpi slender (Fig. 1); propodeum moderately large, in profile not conspicuously larger than metapleuron (Fig. 32); tergite II in profile small, shorter than tergite III (Fig. 1) . . . . . (*Rhynchophion*) . . . . . 2
  - Head, in anterior view, with labiomaxillary complex not exceptionally elongate, but with maxillary palpomere II strongly inflated, subglobose; propodeum in profile exceptionally large, conspicuously larger than and overhanging metapleuron (Figs 27–31); tergite II in profile longer than tergite III (Fig. 2) . . . . . (*Thyreodon*) . . . . . 3
2. Meso- and metasoma blackish; male with claspers quite long and apically obliquely truncate (Fig. 51) . . . . . **1. flammipennis**
  - Meso- and metasoma reddish brown; male with claspers short, apically evenly rounded (Fig. 52) . . . . . **2. woodi**
3. Ocelli very small, the lateral ones separated from orbit by more than their minimum diameter (Fig. 44) . . . . . 4
  - Ocelli larger, the lateral ones closer to eye than their minimum diameter (Figs 41–43) . . . . . 16
4. Metasoma black with tergites III and most of IV lemon-yellow (Fig. 4) . . . . . 5
  - Metasoma mainly all black or dark brown (Figs 3, 5, 6) . . . . . 6
5. Propodeum with a sharp ridge above and behind spiracle (Fig. 20); tergite II, in lateral view, 2.2–2.5 times as long as posteriorly deep; hind femur moderately slender . . . . . **6. laticinctus**
  - Propodeum with upper anterior part convexly rounded, without a distinct sharp ridge above and behind spiracle (Fig. 19); tergite II, in lateral view, 1.6–2.0 times as long as posteriorly deep; hind femur stout . . . . . **7. whitfieldi**
6. Propodeum smooth and polished posteriorly, punctate, without obvious rugae or reticulations (Fig. 33); frons between antennal sockets with a raised, more or less quadrate prominence (Fig. 15) . . . . . **3. santarosae**
  - Propodeum rugose or reticulate, rarely coriaceous posteriorly, but never smooth with punctures (Figs 34–36); frons with a small tubercle between antennal sockets, often with low dorsally divergent carinae (Fig. 16) . . . . . 7
7. Mesosoma orange-brown to reddish brown (cf. Fig. 3) . . . . . 8
  - Mesosoma black (Figs 5, 6) . . . . . 10
8. Propodeum moderately coarsely reticulate with a sharp longitudinal crest above and behind spiracle, and with a distinct zigzag carina extending backwards from this ridge along the lateral margin of the dorsal surface of the propodeum; wings uniformly black (Fig. 13); entire central part of mesopleuron, from upper end of epicnemial carina to hind margin, smooth and polished, impunctate . . . . . **13. zitaniae**
  - Propodeum finely wrinkled, rounded above and behind spiracle, and without a zigzag carina extending backwards laterally; wings black with a central hyaline area (Fig. 14); central part of mesopleuron punctate, except near hind margin . . . . . 9
9. Mesoscutum without a notaular crest (Fig. 46); anterior margin of pronotum with a low, thickened rim; hind leg entirely reddish brown; propodeum dorsally with a shallow median longitudinal furrow . . . . . **1. woodleyi**
  - Mesoscutum with a sharp notaular crest (Fig. 47); anterior margin of pronotum forming a high, thin flange; hind legs more or less entirely black; propodeum dorsally with a very deep longitudinal furrow . . . . . **2. papei**
10. Antenna basally whitish yellow with only apex black . . . . . 11
  - Antenna uniformly dark, at most slightly more brownish yellow basally . . . . . 13
11. Propodeum, in lateral view, with coarse diagonal striae; propodeum with a sharp longitudinal ridge above and behind spiracle (Fig. 28); mesopleuron moderately coarsely closely punctate (Fig. 17) . . . . . **5. morosus**
  - Propodeum, in lateral view, finely reticulate; propodeum rounded above and behind spiracle (Fig. 29); mesopleuron finely and quite sparsely punctate (Fig. 18) . . . . . 12
12. Mesoscutum with a strong transverse crest across anterior part of notaulus (Fig. 45); lower face coriaceous to rugose centrally; pronotum with posterior margin quadrately swollen, not overhanging transverse furrow (Fig. 26) . . . . . **10. walkerae**
  - Mesoscutum with a weak longitudinal swelling along inner periphery of notaulus, without a transverse crest anteriorly (Fig. 49); lower face punctate centrally; pronotum with posterior margin swollen, with an anteriorly directed ridge overhanging transverse furrow (Fig. 49) . . . . . **11. erythroceras**

13. Lower part of occipital carina strong, reaching to base of mandible (Fig. 40); hypostomal carina vestigial; lower part of propleuron with a sharp carina delimiting lower corner (Fig. 50) . . . . . **12. sharkeyi**
- Lower part of occipital carina slightly curved to hypostomal carina, then incomplete, not reaching base of mandible (Fig. 39); hypostomal carina strong; lower part of propleuron without a transverse carina delimiting lower corner (Fig. 49) . . . . . 14
14. Mesopleuron with a sharply impressed, narrow sternal groove; lower part of propleuron convex, peripherally impressed, with a few rugae (Fig. 48) . . . . . **8. deansi**
- Mesopleuron without a distinct sternal groove; lower corner of propleuron unspecialized, rather flat with at most a slightly rugulose margin . . . . . 15
15. Propodeum with three longitudinal furrows, a median one and two sublateral ones; transverse notaular crest quite sharply developed . . . . . **9. apricus**
- Propodeum with only a single median longitudinal furrow (cf. Fig. 35); transverse notaular crest absent . . . . . **4. niger**
16. Mesosoma orange-brown; fore wing hyaline with large blackish areas in basal and marginal cells (Figs 9, 10) . . . . . 17
- Mesosoma black or very dark reddish brown; wings entirely black or black with a central circular clear area (Figs 12–14) . . . . . 18
17. Hind coxa black; male genital capsule with a short, straight, blunt apical spine (Fig. 62); fore wing with basal cell incompletely dark brownish infumate in distal 0.6 (Fig. 9) . . . . . **20. rufothorax**
- Hind coxa red; male genital capsule with an up-flared, slender, apical spine (Fig. 63); fore wing with basal cell entirely dark brownish infumate in distal 0.6 (Fig. 10) . . . . . **21. atriventris**
18. Notauli broad and weakly impressed or indistinct . . . . . 19
- Notauli narrow and strongly impressed (Fig. 37) . . . . . 20
19. Mesopleuron finely but regularly punctate; posterior ocelli large and contiguous with eye (cf. Fig. 43) . . . . . **19. carmeani**
- Mesopleuron smooth and highly polished, impunctate; posterior ocelli separated from eye by about 0.7 times its own maximum diameter . . . . . **14. delvarei**
20. Wings uniformly blue black . . . . . 21
- Wings blackish with a central circular clear area (Fig. 11) . . . . . 22
21. Lateral ocellus contiguous with eye; mesopleuron finely punctate, with epicnemial carina strong, its upper end reaching well above level of lower corner of pronotum; propodeum, in lateral view, reticulate . . . . . **18. darlingi**
- Lateral ocellus separated from eye by about 0.5 times its own maximum diameter; mesopleuron smooth and polished, virtually impunctate, with epicnemial carina laterally absent, its upper end not reaching above level of lower corner of pronotum; propodeum, in lateral view with coarse subparallel diagonal rugae . . . . . **15. schauffi**
22. Lateral ocellus more or less contiguous with the eye (Fig. 41); antenna with flagellum bright yellow . . . . . **16. rivinae**
- Lateral ocellus separated from eye by about 0.5 times its own maximum diameter (Fig. 42); antenna blackish brown . . . . . **17. maculipennis**

transverse, posteriorly slightly concave, with a small median tooth.

*Remarks:* *Rhynchophion* is a small genus restricted to the southern part of the USA and the Neotropical region south to southern Brazil. Three species have been described, *R. flammipennis* Ashmead (USA to Ecuador), *R. ligulifer* (Morley) (Brazil), *R. odontandroplox* Enderlein (Brazil). All are structurally very similar and it has been suggested (Townes, 1971; Gauld, 1985) that all may be colour variants of a single variable species. However, as more becomes known about their biology there is a distinct possibility that they will be found to comprise a complex of sibling species. Two species are present in Costa Rica, the wide-ranging *R. flammipennis* and a

chromatically distinctive new species known only from ACG dry forest. Species of *Rhynchophion* appear to be specialists on the larvae of *Manduca* species (Sphingidae).

#### 1. *RHYNCHOPHION FLAMMIPENNIS* (ASHMEAD)

*Thyreodon flammipennis* Ashmead, 1894: 125. Holotype ♀, MEXICO (CAS) [examined].

*Rhynchophion flammipennis* (Ashmead) Townes, 1945: 746.

Fore wing length 18.3–24.8 mm; clypeus weakly convex, with apex pointed bluntly medially; mandible with lower tooth slightly longer than the upper; malar space 0.7–0.8 times basal mandibular width;

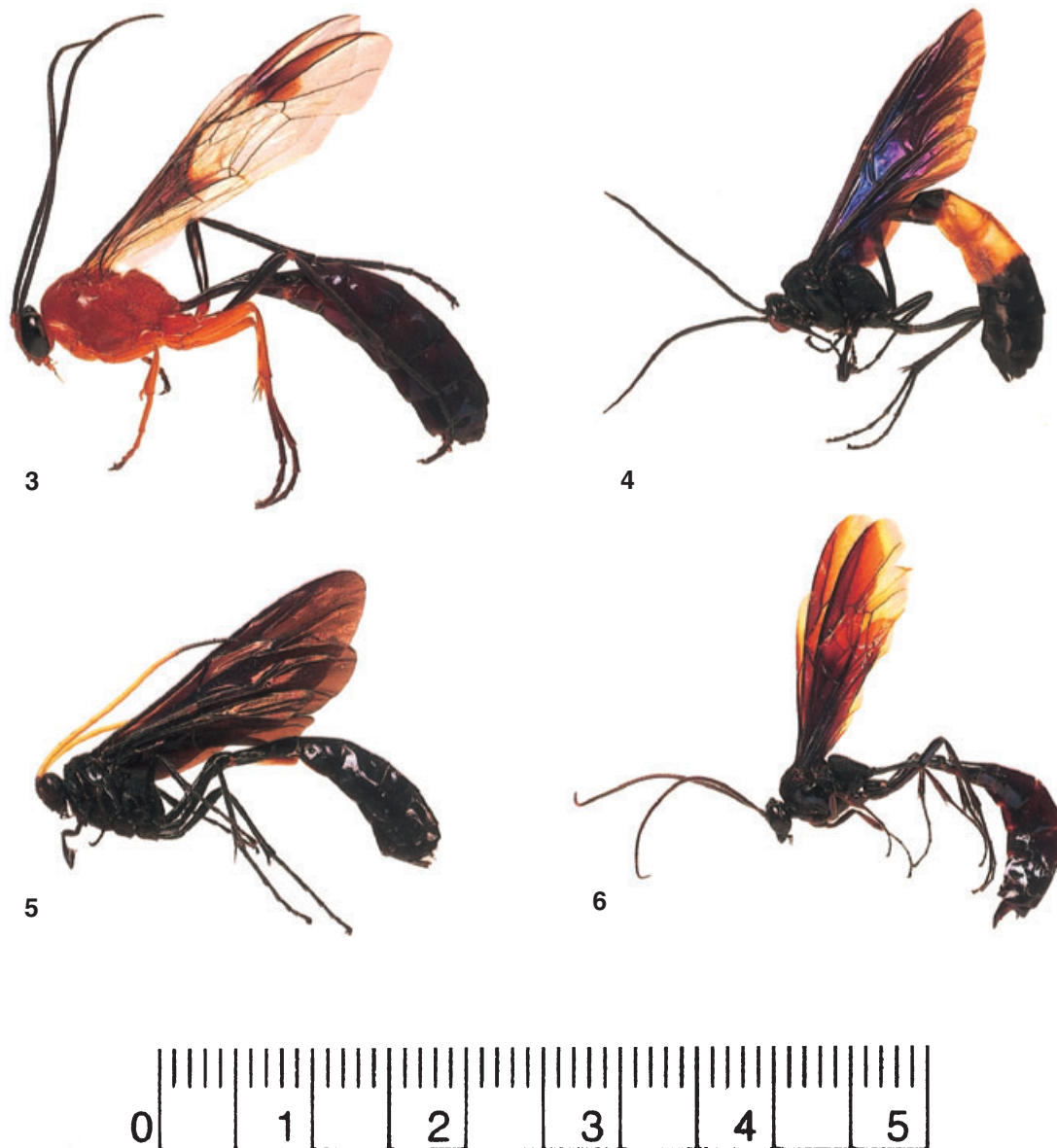


**Figure 2.** Whole insect, lateral. *Thyreodon cyaneus*. Illustration reproduced with the kind permission of the American Entomological Institute.

lower face centrally closely and coarsely punctate; frons with a weakly raised crest between antennal sockets, without a carina extending from outer rim of antennal sockets upwards parallel with eye margin; frons centrally punctate, but with the impressions above the antennal sockets transversely wrinkled; ocelli small, the lateral ocellus separated from eye by about 1.8 times its own maximum diameter; head in dorsal view with gena rather weakly rounded behind eye; antenna setaceous, with 55–60 flagellomeres, the 20th transverse, 0.6–0.7 times as long as broad, the subapical ones with setae that are shorter than the diameter of the flagellomere. Pronotum punctate, with epomia absent; propleuron punctate, with lower corner rounded; mesoscutum closely and coarsely punctate, with black coarse pubescence, scuto-scutellar groove deep but short, laterally margined by raised, simple carinae; scutellum punctate, narrow and convex; mesopleuron closely and quite finely punctate, with epicnemial carina present only ventrally; metapleuron finely and closely punctate; propodeum coriaceous without distinct carinae, although

with wrinkle-like vestiges of lateral longitudinal and lateromedian longitudinal carinae posteriorly. Fore leg of female moderately stout, with 5th tarsomere 0.7–0.8 times as long as preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind tarsomeres 1–4 of male subcylindrical, with moderately long, dense pubescence ventrally. Fore wing with abscissa of *Cu1a* between *Cu1b* and *2m-cu* 1.0–1.1 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*. Metasoma with tergite I moderately stout, anteriorly laterally compressed; tergite II, in lateral view, 1.6–1.8 times as long as posteriorly deep. Male with subgenital plate transverse, convex, covered with fine hair; claspers quite long, the dorsal apex obliquely truncate, the lower margin rounded before apex, and with a deep dorsal notch; aedeagus, in profile, with apex, weakly inflated, distal end slightly flattened, and bordered by a strong lateral keel.

This species has a black body with lower face very slightly brownish, and with antennae yellowish black to rather bright yellow. The wings are strongly yellow,



**Figures 3–6.** Thyreodon species, whole insects, lateral, showing major colour patterns found in the genus. 3. *T. atriventris*. 4. *T. laticinctus*. 5. *T. walkerae*. 6. *T. schauffi*. Scale bar = 5 cm.

basally and apically blackish infumate in most individuals but some are entirely black.

*Remarks:* *Rhynchophion flammipennis* is a very distinctive, stout species that is easily recognized by its colour pattern. Structurally it closely resembles other described species in the genus, but subtle differences in genitalia distinguishes it from the entirely orange-brown *R. woodi* in Costa Rica (see that species). Several individuals collected in Costa Rica differ from typical examples of this species in having the body and wings uniformly black (Figs 7, 8). Structurally they seem to be identical to *R. flammipennis* and the single

reared specimen of this dark morph (96-SRNP-5708) emerged from the same species of host from which a typical specimen was reared (91-SRNP-1336). Here we treat them as simple colour morphs, perhaps induced by different temperature or humidity regimes (e.g. Kettlewell, 1963; Janzen, 1984; Harris, 1987). Similar dark-winged and yellow-winged dichromatism has been observed within species of *Pepsis* (Vardy, 2000), presumed Batesian and Müllerian mimic models for *Rhynchophion*.

*Biological notes:* *Rhynchophion flammipennis* is a very widely distributed species that occurs from the

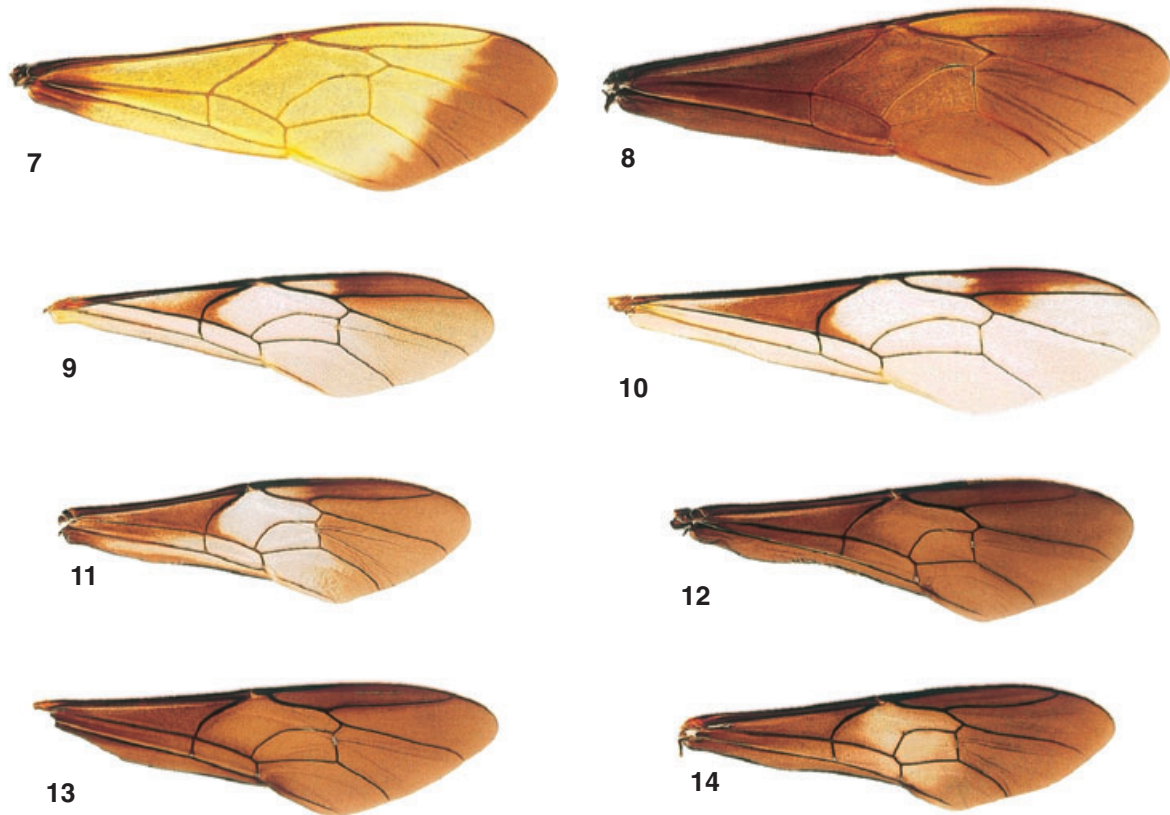


**Table 2.** Known hosts of species in the *Thyreodon* genus-group. Data sources are: JHVC, ichneumonid reared by D. H. Janzen & W. Hallwachs; BMNH and USNM, pinned ichneumonid in museum with host data. Literature references are: 1, Morley (1926); 2, Kester & Tuttle (1999); 3, Peigler (1994); 4, Uchida (1928); 5, Hirayama (1941)

Parasitoid	Host	Source
<i>Euryophion adustus</i>	<i>Lobobunea paratyrrhene</i> Bouvier (Saturniidae)	BMNH
<i>Euryophion latipennis</i>	<i>Bunaea alcinoe caffraria</i> Stoll (Saturniidae)	BMNH
	<i>Imbrasia macrotyhris</i> Rothschild (Saturniidae)	BMNH
	<i>Janomima westwoodi</i> Aurivillius (Eupterotidae)	1
<i>Euryophion</i> (?) <i>ikuthana</i>	<i>Cirina butyrospermi</i> Vület (Saturniidae)	BMNH
	<i>Usta terpsichore</i> (Maassen & Weymer) (Saturniidae)	3
<i>Rhynchophion flammipennis</i>	<i>Manduca lefeburii</i> (Guérin-Méneville) (Sphingidae)	JHVC
	<i>Manduca sexta</i> (L.) (Sphingidae)	2
<i>Rhynchophion woodi</i>	<i>Manduca corallina</i> (Druce) (Sphingidae)	JHVC
	<i>Manduca barnesi</i> (Clark) (Sphingidae)	JHVC
	<i>Manduca rustica</i> (Fab.) (Sphingidae)	JHVC
	<i>Manduca muscosa</i> (Rothschild & Jordan) (Sphingidae)	JHVC
<i>Dictyonotus nigrocyaneus</i>	<i>Lophostethus dumolinii</i> Angas (Sphingidae)	BMNH
<i>Dictyonotus purpurascens</i>	<i>Ampelophaga rubiginosa</i> Bremer & Grey (Sphingidae)	4
	<i>Smerinthus</i> sp. (Sphingidae)	5
<i>Thyreodon woodleyi</i>	<i>Eumorpha satellitia</i> (L.) (Sphingidae)	JHVC
<i>Thyreodon atricolor</i>	<i>Lapara bombycoides</i> Walker (Sphingidae)	USNM
	<i>Lapara coniferarum</i> (Smith) (Sphingidae)	USNM
	<i>Paonias excaecatus</i> (Smith) (Sphingidae)	USNM
<i>Thyreodon santarosae</i>	<i>Orthorene purpurascens</i> (Schaus) (Saturniidae)	JHVC
	<i>Orthorene verana</i> (Schaus) (Saturniidae)	JHVC
	<i>Ptiloscota dargei</i> Lemaire (Saturniidae)	JHVC
	<i>Syssphinx mexicana</i> (Boisduval) (Saturniidae)	JHVC
	<i>Syssphinx molina</i> (Cramer) (Saturniidae)	JHVC
	<i>Syssphinx colla</i> (Dyar) (Saturniidae)	JHVC
	<i>Syssphinx quadrilineata</i> (Grote & Robinson) (Saturniidae)	JHVC
<i>Thyreodon laticinctus</i>	<i>Xylophanes anubus</i> (Cramer) (Sphingidae)	JHVC
<i>Thyreodon whitfieldi</i>	<i>Xylophanes chiron</i> Drury (Sphingidae)	JHVC
<i>Thyreodon walkerae</i>	<i>Xylophanes hannemanni</i> Closs (Sphingidae)	JHVC
<i>Thyreodon erythrocerca</i>	<i>Aellopus titan</i> (Cramer) (Sphingidae)	JHVC
	<i>Eupyrrhoglossum sagra</i> (Poey) (Sphingidae)	JHVC
<i>Thyreodon apricus</i>	<i>Erinnyis lassauxii</i> (Boisduval) (Sphingidae)	JHVC
<i>Thyreodon sharkeyi</i>	<i>Xylophanes turbata</i> (Edwards) (Sphingidae)	JHVC
	<i>Xylophanes pluto</i> (Fab.) (Sphingidae)	JHVC
<i>Thyreodon maculipennis</i>	<i>Perigonia lusca</i> (F.) (Sphingidae)	JHVC
	<i>Perigonia ilus</i> Boisduval (Sphingidae)	JHVC
<i>Thyreodon schauffi</i>	<i>Callionima denticulata</i> (Schaus) (Sphingidae)	JHVC
<i>Thyreodon rufothorax</i>	<i>Pachygonidia drucei</i> (Rothschild & Jordan) (Sphingidae)	JHVC
	<i>Pachylioides resumens</i> (Walker) (Sphingidae)	JHVC
<i>Thyreodon atriventris</i>	<i>Pachylia ficus</i> (L.) (Sphingidae)	JHVC
	<i>Pachylia syces</i> (Hübner) (Sphingidae)	JHVC

south-western USA south to Ecuador and possibly northern Argentina. In Costa Rica this species has only been collected in the seasonally dry north-west of the country, where it occurs from sea-level up to about

800 m. Adults appear in the first third of the rainy season (June to early August). Capture dates in Santa Rosa are given in Figure 64. Despite intensive sampling in the ACG dry forest, it has never ever been col-



**Figures 7–14.** Fore wings, showing colour patterns. 7, *Rhynchophion flammipennis*, normal form. 8, *Rhynchophion flammipennis*, dark form. 9, *Thyreodon rufothorax*. 10, *T. atriventris*. 11, *T. maculipennis*. 12, *T. walkerae*. 13, *T. zitaniae*. 14, *T. papei*.

lected outside this short season (when the vast majority of the sphingid host caterpillar population has its single annual generation), and we conclude that it is univoltine.

*Rhynchophion flammipennis* is the only black and orange 'Pepsis mimic' among the Costa Rican *Thyreodon* group. It is rarely encountered flying energetically and rapidly in the daytime through brushy edges of secondary successional dry forest in Sector Santa Rosa, ACG. It visits at least the white sprays of fly and wasp-pollinated flowers of *Allophylus occidentalis* (Sapindaceae), *Forsteronia spicata* (Apocynaceae) and *Trigonia rugosa* (Trigoniaceae). All collections in Costa Rica have been with butterfly nets, Malaise traps or rearing in the dry forests and their margins in the Pacific side of the ACG. It does not appear at light traps placed in the same ACG dry forests. We conclude that it does not occur in ACG rain forest.

The ACG larval hosts are all *Manduca lefeburii* (Table 2) feeding on *Casearia corymbosa* (Flacourtiaceae). What appears to be the same species has been reared once from *Manduca sexta* in the south-western USA (Kester & Tuttle, 1999). A total of ten *Rhynchophion* cocoons, all noticeably larger than those of

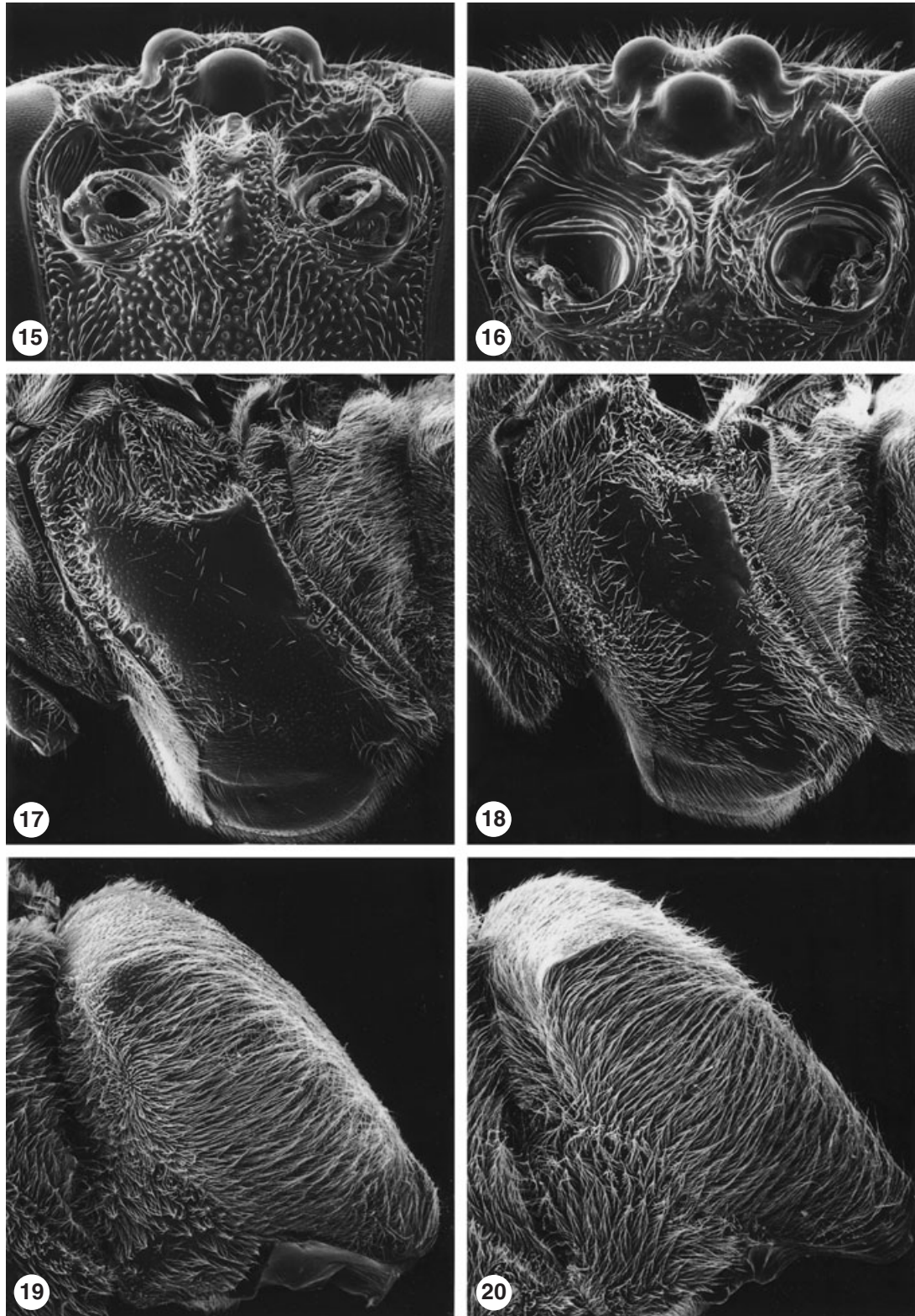
*R. flammipennis*, have been reared from four other species of *Manduca* in the ACG dry forest, but only one enclosed (*R. woodi*) (Table 2). Our preliminary hypothesis is that in the ACG, *R. flammipennis* is a specialist on *Manduca lefeburii* whereas *R. woodi* is a *Manduca* generalist.

In both successful rearings of *R. flammipennis*, it remained dormant in the cocoon through the remaining 65% of the rainy season and nearly all of the 6-month dry season. The time between cocoon spinning and eclosion was 354 and 339 days.

*R. flammipennis* cocoons have the same distinctive structure as those of *Thyreodon* (see detailed description for *Thyreodon walkerae* below) but are slightly more cylindrical with a lesser bulge in the middle. The wasp cuts a round exit hole 2–4 mm in diameter through the end of the cocoon.

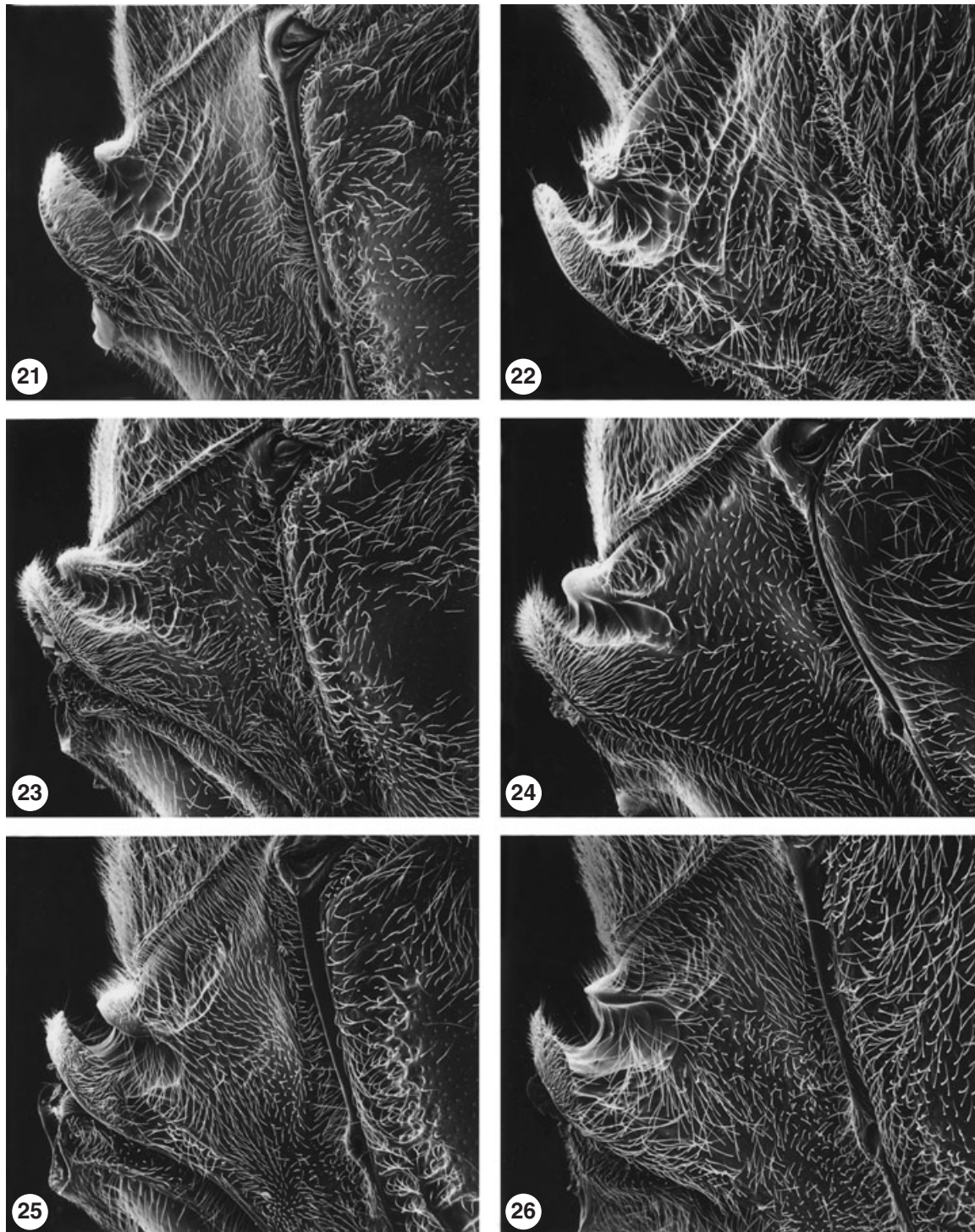
**Material examined:** Holotype ♀, MEXICO: Baja California, El Taste, 1100 m (CAS).

Non-type material: ARGENTINA: 1 ♀, 1 ♂, no further data, 1904 (*Thomas*) (BMNH). COSTA RICA: Guanacaste Prov.: 1 ♀, Barra Honda National Park, dry forest, 100 m, vi.1988 (*Gauld & Mitchell*)



**Figures 15–20.** SEM photographs of *Thyreodon* spp. 15–16, head, anterior, showing interantennal area; 15, *T. santarosae*; 16, *T. walkerae*. 17–18, mesopleuron, lateral; 17, *T. morosus*; 18, *T. walkerae*. 19–20, propodeum, lateral; 19, *T. whitfieldi*; 20, *T. laticinctus*.



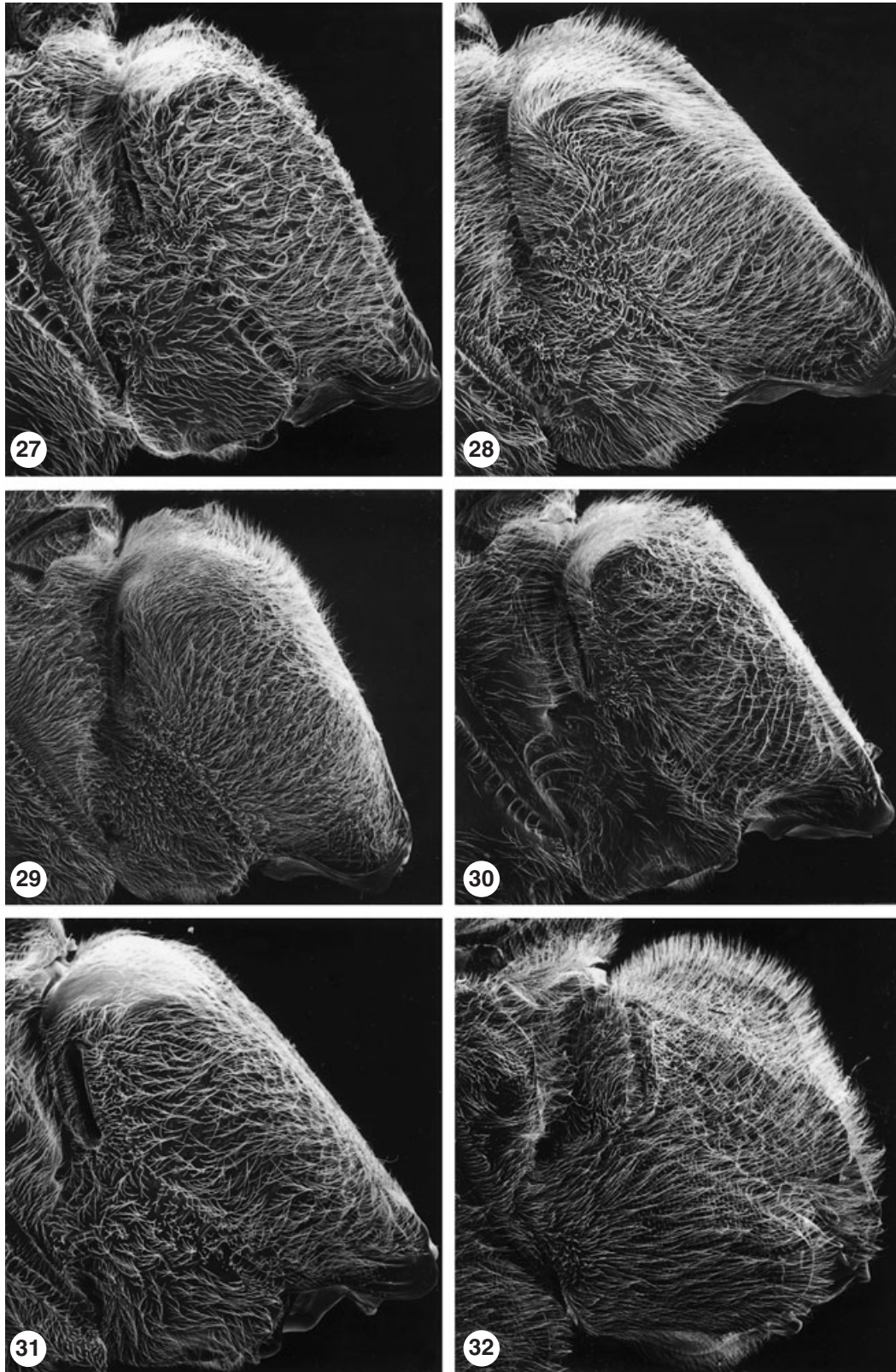


**Figures 21–26.** SEM photographs of *Thyreodon* spp., pronotum, lateral; 21, *T. whitfieldi*; 22, *T. laticinctus*; 23, *T. darlingi*; 24, *T. rivinae*; 25, *T. morosus*; 26, *T. walkerae*.

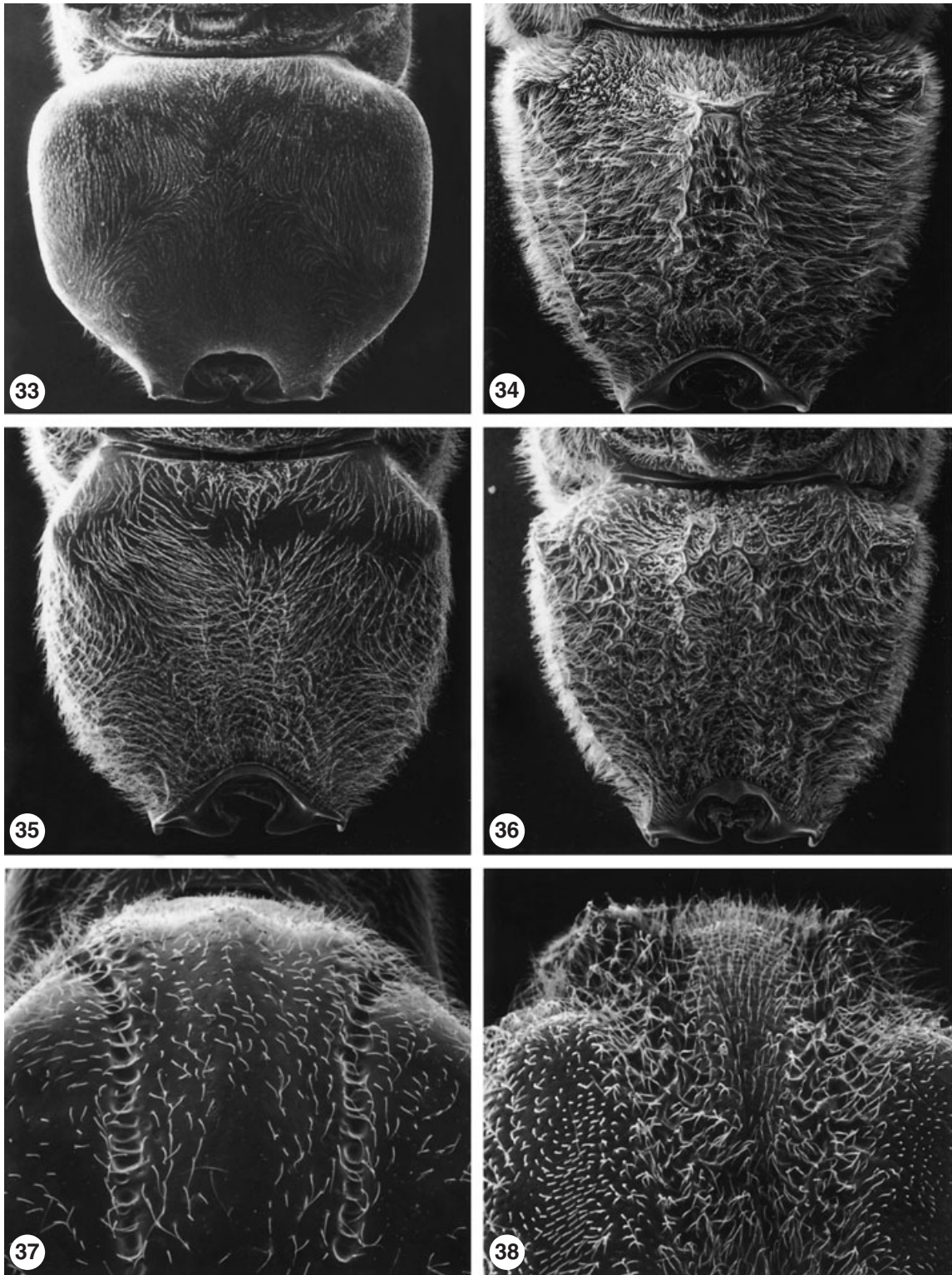
(BMNH); 1 ♂, Guanacaste National Park, reared as per data above (*Janzen & Hallwachs*) (JHVC); 1 ♀, 18 ♂, Guanacaste National Park, Casa Mariksa [= Estacion Maritza], 560 m, vi–vii.1986–88 (*Gauld*

& *Mitchell*) (AEIC, BMNH); 3 ♂, Guanacaste National Park, Estacion Maritza, 600 m, vii.1989, vi.1990 (*Parataxonomists*) (INBio); 1 ♀, 1 ♂, Rincon de la Vieja National Park, Las Pailas, 800 m,



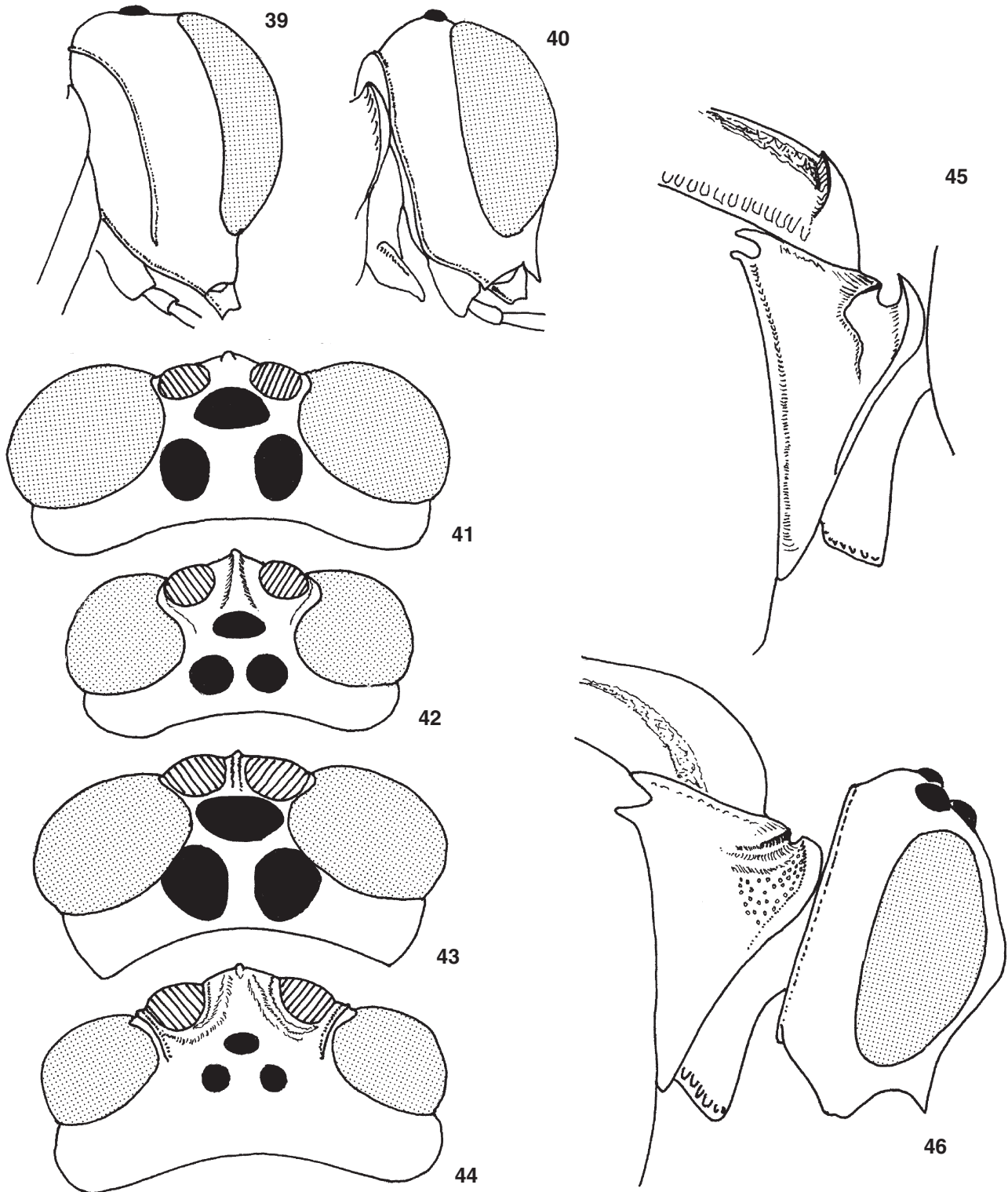


**Figures 27–32.** SEM photographs of propodeum lateral. 27, *Thyreodon darlingi*; 28, *T. morosus*; 29, *T. walkerae*; 30, *T. zitaniae*; 31, *T. rivinae*; 32, *Rhynchophion flammipennis*.

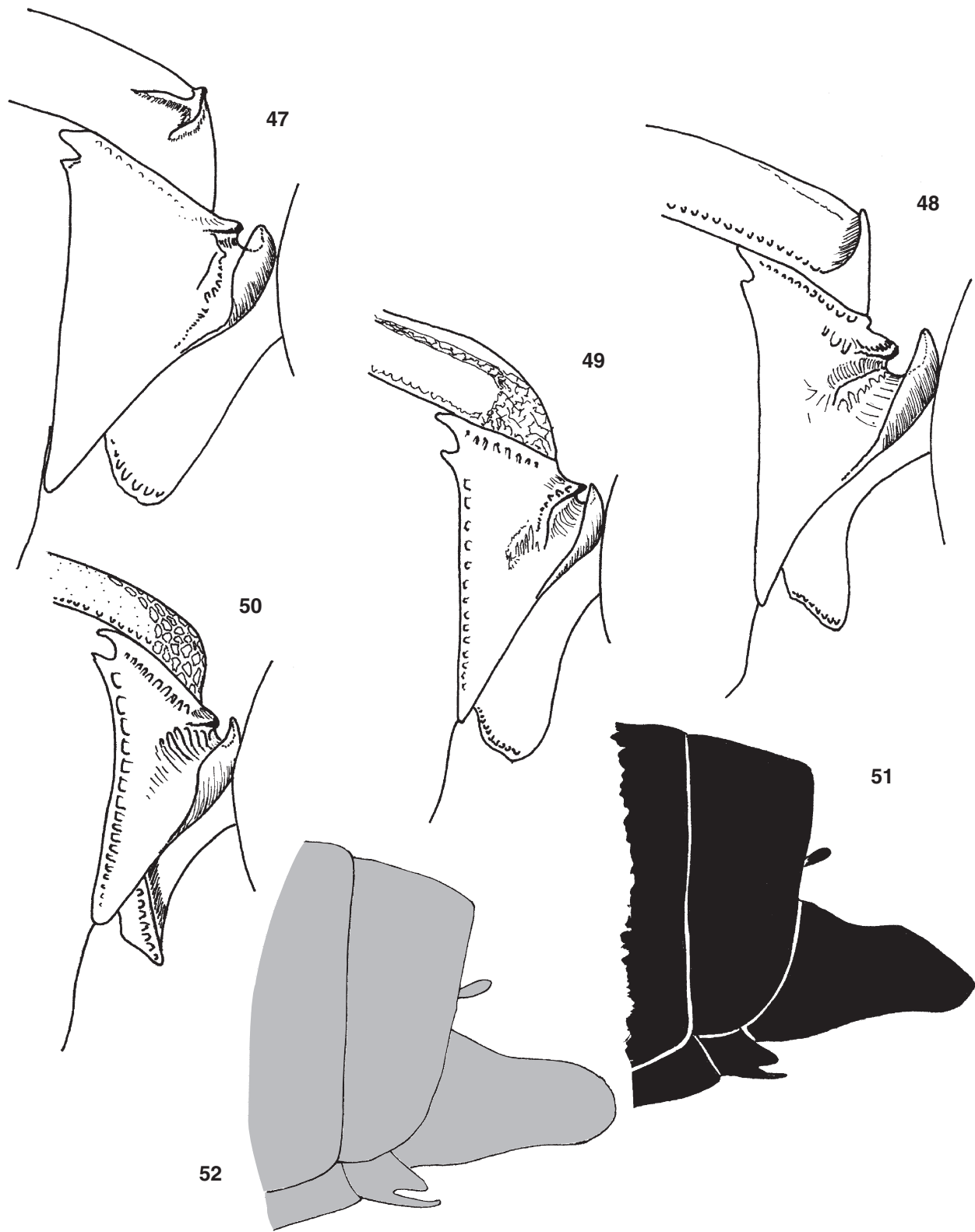


**Figures 33–38.** SEM photographs of *Thyreodon* spp. 33–36, propodeum, dorsal; 33, *T. santarosae*; 34, *T. atriventris*; 35, *T. rivinae*; 36, *T. darlingi*. 37–38, mesoscutum dorsal; 37, *T. darlingi*; 38, *T. walkerae*.



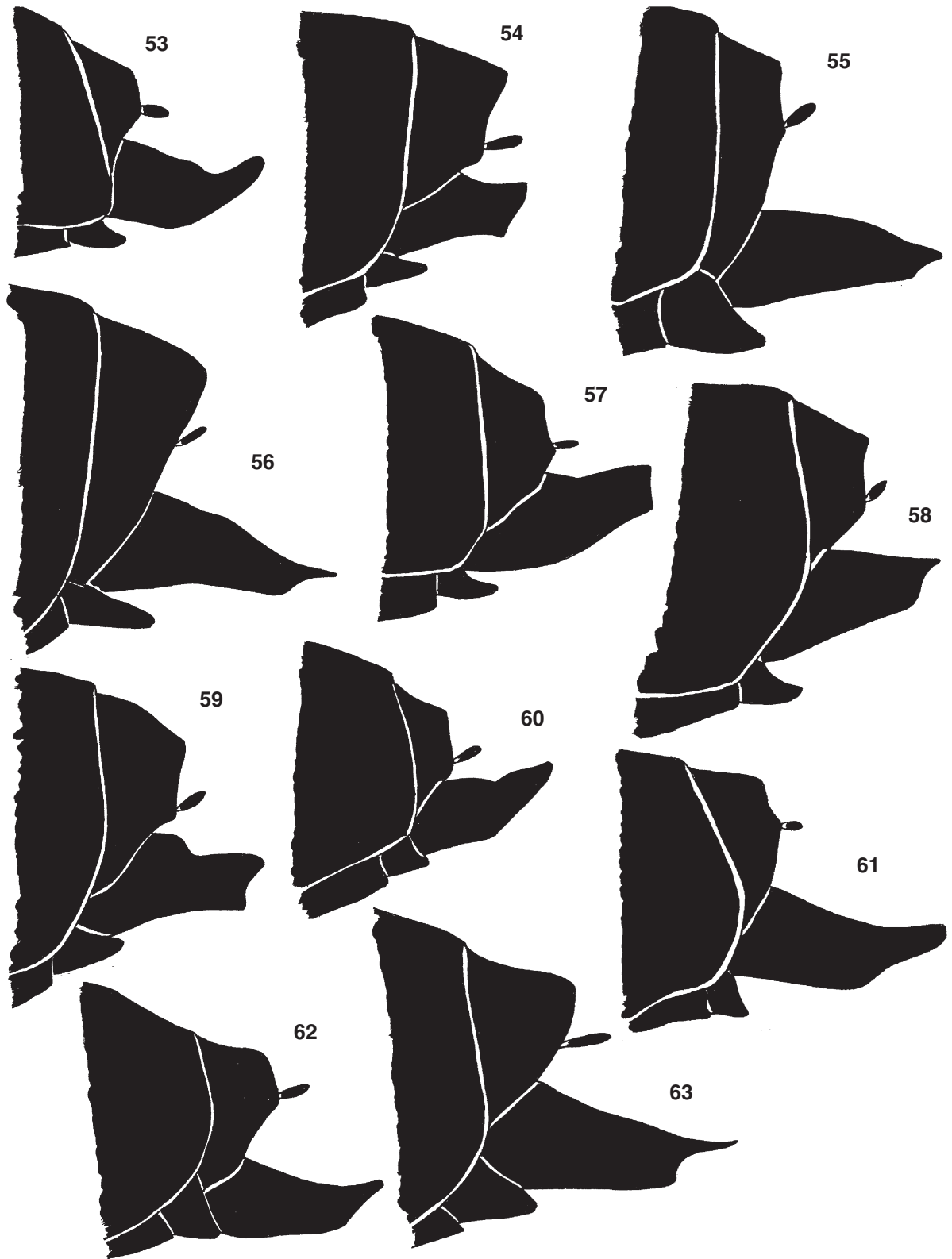


**Figures 39–46.** *Thyreodon* species. 39–40, head, postero-lateral; 39, *T. erythroceras*; 40, *T. sharkeyi*. 41–44, head, dorsal; 41, *T. rivinae*; 42, *T. maculipennis*; 43, *T. atriventris*; 44, *T. woodleyi*. 45–46, mesoscutum and pronotum, lateral; 45, *T. walkerae*; 46, *T. woodleyi*.

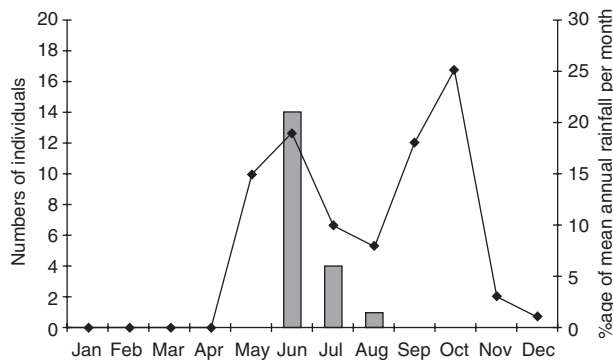


**Figures 47–52.** 47–50, mesoscutum and pronotum, lateral; 47, *T. papei*; 48, *T. deansi*; 49, *T. erythroceras*; 50, *T. sharkeyi*. 51–52, apex of metasoma and male genital capsule, lateral; 51, *Rhynchophion flammipennis*; 52, *R. woodi*.





**Figures 53–63.** Apex of metasoma and male genital capsule, lateral; 53, *T. maculipennis*; 54, *T. erythrocerata*; 55, *T. whitfieldi*; 56, *T. laticinctus*; 57, *T. zitaniae*; 58, *T. papei*; 59, *T. morosus*; 60, *T. schauffi*; 61, *T. darlingi*; 62, *T. rufothorax*; 63, *T. atriventris*.



**Figure 64.** The total numbers of individuals of *Rhynchophion flammipennis* collected by month in Malaise traps in the Bosque Humedo, Bosque San Emilio and Administration Area of Sector Santa Rosa of the ACG compared with the monthly percentage of the annual rainfall. Traps were operated continuously for three consecutive years, 1985–87.

vii.1993, vi.1994 (*Taylor & Rodriguez*) (INBio); 1 ♂, Rincon de la Vieja National Park, Estacion Las Pailas, 800 m, vii–viii.1992 (*Garcia*) (INBio); 4 ♀, 12 ♂, Santa Rosa National Park, 300 m, vi.1977–vii.1987 (*Janzen & Gauld*) (BMNH); 3 ♂, same locality, 300 m, vii.1992 (*Parataxonomists*) (INBio). MEXICO: Guerrero: 1 ♂, Sierra de las Aguas Escondidas, vii. (*Smith*) (BMNH); 1 ♀, 4 ♂, Xucumantlan, 230 m, vii (*Smith*) (BMNH).

All black individuals: COSTA RICA: Guanacaste Prov.: 1 ♂, Barra Honda National Park, dry forest, 100 m, vi.1988 (*Gauld & Mitchell*) (BMNH); 3 ♂, Guanacaste National Park, Estacion Maritza, 560 m, vi.1987 (*Gauld & Mitchell*) (BMNH); 1 ♂, Guanacaste National Park, reared as per data above, vi.1986 (*Janzen & Hallwachs*) (JHVC).

## 2. *RHYNCHOPHION WOODI* GAULD SP. NOV.

Fore wing length 23.9 mm; clypeus weakly convex, with apex pointed bluntly medially; mandible with lower tooth slightly longer than the upper; malar space 0.7–0.8 times basal mandibular width; lower face centrally closely and coarsely punctate; frons with a weakly raised crest between antennal sockets, without a carina extending from outer rim of antennal sockets upwards parallel with eye margin; frons centrally punctate, but with the impressions above the antennal sockets transversely wrinkled; ocelli small, the lateral ocellus separated from eye by about 1.8 times its own maximum diameter; head in dorsal view with gena rather weakly rounded behind eye; antenna setaceous, with 55–64 flagellomeres, the 20th transverse, 0.6 times as long as broad, the subapical ones with setae which are shorter than the diameter of the flagello-

mere. Pronotum punctate, with epomia absent; propleuron punctate, with lower corner rounded; mesoscutum closely and coarsely punctate, with black coarse pubescence, scuto-scutellar groove deep but short, laterally margined by raised, simple carinae; scutellum punctate, moderately broad and weakly convex; mesopleuron closely and quite finely punctate, with epicnemial carina present only ventrally; metapleuron finely and closely punctate; propodeum coriaceous without distinct carinae, although with wrinkle-like vestiges of lateral longitudinal and lateromedian longitudinal carinae posteriorly. Fore tarsal claw long and with fine, close pectinae; hind tarsomeres 1–4 of male distinctly compressed with short, dense pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.2 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I stout, anteriorly laterally compressed; tergite II, in lateral view, 1.1 times as long as posteriorly deep. Male with subgenital plate transverse, convex, covered with fine hair; claspers short, the dorsal apex rounded, the lower margin rounded before apex, and with a deep dorsal notch; aedeagus, in profile, with apex weakly inflated, slightly flattened, with a strong lateral keel.

A reddish brown species with antennae yellowish brown; wings strongly yellow, basally and apically blackish infumate.

**Remarks:** This species is named in honour of D. Monty Wood, in recognition of his decades of identification of thousands of tachinid flies reared by the ACG caterpillar inventory. *Rhynchophion woodi* is a very distinctive species that is easily recognized by its entirely reddish brown colour pattern. It appears to be a *Polistes canadensis* L. (Vespidae) mimic. Structurally it is very similar to *R. flammipennis*, but the scutellum is more weakly convex and rather broader, and the hind tarsus of the male is distinctly and distinctively laterally compressed. The claspers are of a completely different shape, being shorter than those of *R. flammipennis*, and apically rounded rather than obliquely truncate (Figs 51, 52). It is also larger than *R. flammipennis*.

**Biological notes:** The unique male of *R. woodi* was reared from the larva of *Manduca barnesi* feeding on a 2-m-tall sapling of *Godmania aesculifolia* (Bignoniaceae) in ACG dry forest [93-SRNP-1755]. The caterpillar became a prepupa in early June. The parasitoid larva emerged 3 days later and spun a typical *Rhynchophion* cocoon in which the wasp remained until it emerged as an adult the following June. In nine other cases, a *Manduca* caterpillar produced a large larva, large enough to spin the very large cocoon made by *Rhynchophion woodi*, but the wasp always died. It may be that the wasp prepupae or pupae died of desiccation in the very dry rearing conditions (empty

glass bottles), being in cocoons that appear to be less thick-walled and presumably less desiccation-resistant than are the cocoons of *Thyreodon*. This speculation is reinforced by the fact that *Manduca* pupal chambers are usually 5–10 cm underground, and therefore more humid during the dry season, than are the pupal chambers of the species of sphingids and saturniids parasitized by *Thyreodon*, which are made in the litter and on the soil surface.

*Material examined*: Holotype ♂, COSTA RICA: Guanacaste Prov.: Sector Santa Rosa, ACG, 300 m, vi.1994 (Janzen & Hallwachs) (JHVC).

#### THE GENUS *THYREODON* BRULLÉ

*Thyreodon* Brullé, 1846: 150. Type species: *Thyreodon cyaneus* Brullé, by subsequent designation, Hooker, 1912: 107.

*Athyreodon* Ashmead, 1900: 87. Type species: *Athyreodon thoracicus* Ashmead (= *Ophion atriventris* Cresson), by original designation.

*Diagnosis*: Large, slender to moderately stout insects, fore wing length 15.2–27.8 mm, black, black and yellow, metallic blue, red-brown or orange and black in colour with blackish or mottled wings (Figs 3–6). Head in anterior view with labio-maxillary complex not elongate, barely projecting ventrally; maxillary palp with palpomere II grossly inflated and often slightly flattened; clypeus with margin out-flared, thin, centrally with an obtuse to moderately acute point; ocelli from small, the lateral ones separated from eye by more than their own diameter, to very large, the lateral ones contiguous with the eye; occipital carina complete dorsally, ventrally usually not reaching hypostomal carina, rarely joining it. Antenna short and moderately stout, setaceous, the central flagellomeres from slightly elongate to strongly transverse. Pronotum with hind margin mediodorsally thickened and subquadrate in profile, sometimes with upper anterior margin projecting strongly forwards, often with anterior margin reflexed; notauli usually sharply impressed and reaching beyond centre of mesoscutum; lateral part of metanotum weakly swollen and not carinate; propodeum grossly inflated, overhanging a reduced metapleuron, posteriorly, mediodorsally with a shallow to very deep median longitudinal furrow. Hind coxa small, its apex more or less level with hind margin of propodeum. Fore wing with abscissa of vein *1m-cu* distal to bulla longer than abscissa of *M* between *2m-cu* and *3rs-m*. Metasoma with tergite II slightly to obviously longer than tergite III; male with dorsal margin of clasper weakly to strongly notched; aedeagus simple or with a sharp subapical lateral keel; male subgenital plate slightly elongate, posteriorly convex, sometimes thickened.

*Remarks*: *Thyreodon* is primarily Neotropical, although one species occurs in the Nearctic as far north as southern Canada where it is recorded as a parasitoid of *Lapara coniferarum*, *L. bombycoides* and *Paonias excaecatus* (Sphingidae) (Hooker, 1912). Four other species, *T. fernaldi* Hooker, *T. ornatipennis* Cresson, *T. apricus* and *T. rivinae*, also extend from Mexico into the southern USA (Carlson, 1979; Porter, 1980, 1984). *Thyreodon* is the most species-rich genus in the genus-group, and includes many more species than all the other genera combined. It is well represented in Central America, and 21 species have been found in Costa Rica. However, there may be hundreds more in South America, including the widely distributed type-species *T. cyaneus* (Fig. 2). Despite collecting efforts embracing hundreds of Malaise trap years in all Costa Rican ecosystems and habitats (Hanson & Gauld, 1995), about 55% of the Costa Rican species have never been collected in Malaise traps. Furthermore, careful observations of host range coupled with close morphological examination has shown that several fairly well-known, slightly variable species, such as '*T. atriventris*' and '*T. laticinctus*', are in reality complexes of morphologically quite uniform, similar species, each parasitizing different but fully sympatric species of hosts.

#### 1. *THYREODON WOODLEYI* GAULD SP. NOV.

Fore wing length 20.4 mm; clypeus convex, with apex strongly pointed medially and conspicuously flared outwards; malar space 0.6 times basal mandibular width; maxillary palp long with second palpomere broadened and flattened; lower face centrally closely and coarsely punctate; frons with a pair of dorsally divergent crests between antennal sockets and with a sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli small, the lateral ocellus separated from eye by about 1.8 times its own maximum diameter; head in dorsal view closely punctate, with gena weakly rounded behind eye, occipital carina strong, its lower end sharp, not reaching hypostomal carina; antenna setaceous, with 61 flagellomeres, the 20th transverse, 0.8 times as long as broad, the subapical ones with setae which are shorter than the diameter of the flagellomere. Pronotum short with anterior margin slightly thickened, not reflexed, and with posterior margin centrally swollen, forming a sharp angular keel which is separated from the anterior margin by a deep U-shaped groove; epomia weak but discernible on upper part of pronotum; propleuron closely and coarsely punctate, slightly convex, with lower corner flattened but not peripherally impressed; mesoscutum finely and closely punctate, with broad, shallow, reticulated notauli that are confluent posteriorly, inner anterior margin of notaulus unspecialized;

scuto-scutellar groove very deep, laterally margined by a very strongly raised, ridged carina; scutellum with close, coarse punctures, convex; mesopleuron closely and coarsely punctate, without a sternal impression; metapleuron finely and closely punctate with a few ridges anteriorly; propodeum laterally weakly flattened, anteriorly punctate grading to finely reticulate, rounded and without a ridge above and behind the spiracle; propodeum posterodorsally finely reticulate, centrally with a shallow longitudinal impression. Fore leg of female rather stout, with coxa with a bluntly rounded protuberance behind trochantal insertion, with 5th tarsomere about 0.9 times as long as preceding two tarsomeres, with tarsal claw long and with close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 6 times as long as maximally deep. Fore wing with abscissa of *Cu1a* between *Cu1b* and *2m-cu* 1.1 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*. Metasoma with tergite I moderately slender, anteriorly slightly compressed; tergite II, in lateral view, 2.0 times as long as posteriorly deep. Male unknown.

A reddish brown species with lateral parts of tergites II–IV obscurely infuscate; wings strongly yellowish, with distal apices broadly blackish infumate.

*Remarks:* *Thyreodon woodleyi* is named in honour of Norman E. Woodley, in recognition of decades of identification of thousands of species of *Belvosia* (Tachinidae) reared by the ACG caterpillar inventory. *T. woodleyi* is a very distinctive species that is easily recognized by its colour pattern alone because no other species of *Thyreodon* in Costa Rica is uniformly reddish brown, although it superficially resembles *Rhynchophion woodi* described above. Morphologically it is strikingly distinct from other species in having the anterior margin of the pronotum slightly thickened, but not at all reflexed (Fig. 46). These two traits suggest that *T. woodleyi* is one of the most basal species in the genus. Interestingly, both it and *T. papei* (another rather basal species) have yellowish wings with black apices, as do most species of *Dictyonotus* (Old World) and *Rhynchophion*, suggesting that this colour pattern may be a ground plan trait of the *Thyreodon* genus-group.

*Biological notes:* *Thyreodon woodleyi* is only known from a single individual that was reared from the larva of *Eumorphia satellitia* (Sphingidae: Macroglossinae) collected in seasonally dry forest in north-western Costa Rica. The caterpillar was found feeding on *Cissus pseudosicyoides* (Vitaceae) and became a prepupa on 31 May 1999, when it was consumed by the wasp larva. The wasp larva spun a cocoon from which an adult emerged on 7 July 1999 [99-SRNP-7477]. Two other *Thyreodon* larvae emerged from the

same species of caterpillar in the same dry forest in the same season, each spinning the same massive cocoon as the one that eclosed. It is particularly striking that more than 12 Malaise trap years of collecting from the immediate vicinity of this rearing did not capture a single individual of *T. woodleyi*. Furthermore, 441 wild-caught caterpillars of *Eumorphia satellitia* in this habitat, and 1026 wild-caught caterpillars of five species of *Eumorphia* in the ACG over 24 years produced only these three *Thyreodon* cocoons.

*Material examined:* Holotype ♀, COSTA RICA: Guanacaste Prov.: Area Administrativa, Sector Santa Rosa, ACG, vii.1999 (*Janzen & Hallwachs*) (JHVC).

## 2. *THYREODON PAPEI* GAULD SP. NOV.

Fore wing length 19.3–20.0 mm; clypeus convex, with apex pointed medially; malar space about 0.6–0.7 times basal mandibular width; maxillary palp long with second palpomere broadened and slightly flattened; lower face centrally punctate, with a few scattered rugae; frons with a strong median vertical ridge between antennal sockets, the upper part of which tends to form a pair of divergent carina-like rugae, and with sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally finely rugose; ocelli small, the lateral ocellus separated from eye by 1.4–1.5 times its own maximum diameter; head in dorsal view unusually coarsely punctate, with gena rather broad, evenly rounded behind eye, occipital carina strong, its lower end sharp, in-turned, not reaching hypostomal carina; antenna setaceous, with 61–66 flagellomeres, the 20th transverse, 0.8 times as long as broad, the subapical ones with setae which are shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, centrally impressed ridge which is separated from the anterior margin by a deep U-shaped groove; epomia strong on upper part of pronotum forming a lateral ridge that curves forwards to reach beneath reflexed anterior margin; propleuron sparsely punctate, with lower corner very weakly expanded, peripherally shallowly impressed; mesoscutum closely and quite coarsely punctate, with broad, shallow, reticulate notauli that are more or less confluent posteriorly, inner anterior margin of notaulus raised to form a more or less transverse crest across the notaulus; scuto-scutellar groove very deep, laterally margined by very strongly raised carinae; scutellum closely and moderately coarsely punctate, convex; mesopleuron closely and quite coarsely punctate, without a sharp sternal impression; metapleuron puncto-coriaceous; propodeum laterally slightly flattened, finely rugose-striate, angularly rounded above and



behind the spiracle; propodeum posterodorsally finely rugose/coriaceous, centrally with a single moderately broad deep longitudinal impression. Fore leg of female stout, with coxa with a low and bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 1.3–1.4 times as long as preceding two tarsomeres, with tarsal claw very long and with short, close pectinae; hind coxa in profile moderately small, its hind end projecting to about level of hind end of propodeum; hind femur slender, 5–6 times as long as maximally deep; hind tarsus of male with dense, long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.85–0.90 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly subcylindrical; tergite II, in lateral view, 2.2–2.4 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers quite long, the dorsal apex obliquely truncate, the upper corner produced into a small sharp projection, the lower margin weakly convex (Fig. 58); aedeagus in profile with apex expanded, rounded on extreme apex, without a sharp lateral keel.

Head orange-brown, with interocellar area, vertex and frons blackish; flagellum black; mesosoma orange-brown; metasoma shining black. Anterior two pairs of legs orange brown, mid tarsus blackish; hind legs black; wings weakly yellowish infumate centrally, darkly infumate proximally and to a lesser extent distally as well.

*Remarks:* *Thyreodon papei* is named in honour of Thomas Pape, in recognition of his identification of all of the sarcophagid flies reared by the ACG caterpillar inventory. *T. papei* is structurally and in colour similar to *T. zitaniae*. Both species have rather small ocelli, and have an orange mesosoma and black metasoma. They differ in several respects, however. *T. papei* has a sharp notaular crest on the mesoscutum, has the propodeum rounded above and behind the propodeal spiracle, and has a central hyaline area on the fore wing; by contrast, *T. zitaniae* has the mesoscutum without any trace of a notaular crest, has a sharp ridge above and behind the propodeal spiracle, and has the fore wings uniformly black. *T. papei* also has the second discal cell in the fore wing shorter, with the abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.85–0.90 times as long as the abscissa of *Cu*1 between *cu-a* and *1m-cu*. In *T. zitaniae* this vein is 1.2–1.3 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. *T. papei* also has the fore leg unusually stout, with 5th tarsomere long, 1.3–1.4 times as long as the preceding two tarsomeres, whereas in *T. zitaniae* the 5th tarsomere is only 0.5–0.6 times as long as the preceding two tarsomeres.

*Biological notes:* *Thyreodon papei* is only known to occur in Costa Rica. Three free-flying adults have been

collected in the ACG rain forest on the lower slopes of Volcán Orosi and Volcán Rincon de la Vieja, well within the area of the ACG caterpillar rearing programme, but it has not yet been encountered in many thousands of caterpillars and many tens of sphingid species reared from these sites.

*Material examined:* Holotype ♂, COSTA RICA: Guanacaste Prov.: Rincon de la Vieja National Park, Estacion Las Pailas, 800 m, v–vi.1993 (Taylor) (INBio). Paratypes: COSTA RICA: Guanacaste Prov.: 1 ♂, Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, iii.1990 (Rios & Moraga) (INBio); 1 ♀, Rincon de la Vieja National Park, Estacion Las Pailas, 800 m, iv.1994 (Taylor) (INBio).

### 3. *THYREODON SANTAROSAE* PORTER

*Thyreodon santarosae* Porter, 1986: 133. Holotype ♂, COSTA RICA (USNM) [examined].

Fore wing length 17.2–21.8 mm; clypeus convex, with apex pointed medially; malar space 0.4–0.5 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and flattened; lower face centrally coarsely punctate; frons with a raised quadrate prominence between antennal sockets and with a high, rather blunt carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose, but with the impressions above the antennal sockets transversely striate; ocelli small, the lateral ocellus separated from eye by about 1.3 times its own maximum diameter; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end not reaching hypostomal carina; antenna setaceous, with 62–64 flagellomeres, the 20th transverse, 0.6–0.7 times as long as broad, the subapical ones with setae which are shorter than the diameter of the flagellomere. Pronotum short with anterior margin thickened and weakly reflexed, and with posterior margin centrally quadrately swollen, forming an angular projecting ridge which is separated from the anterior margin by a deep U-shaped groove; epomia absent; propleuron sparsely punctate, with lower corner rounded, peripherally with a few coarse punctures above lower corner; mesoscutum moderately coarsely punctate, with broad, very shallow, reticulated notauli that are confluent posteriorly, inner anterior margin of notaulus unspecialized; scuto-scutellar groove deep but short, laterally margined by raised, simple carinae; scutellum punctate, broad and convex; mesopleuron moderately closely and quite coarsely punctate, without a sternal impression; metapleuron finely punctate with a few obscure diagonal ridges; propodeum slightly globose, laterally not flattened, punctate, without a ridge above and behind

the spiracle; propodeum posterodorsally smooth with scattered punctures, centrally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa with a low, bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 1.2–1.3 times as long as preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 5 times as long as maximally deep; hind tarsus of male with moderately short, dense pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.7–0.8 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I moderately slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 1.5–1.6 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with fine hair; claspers quite long, the dorsal apex obliquely truncate, the lower margin rounded before apex, and with a very shallow, broad dorsal notch; aedeagus on profile with apex up-turned, weakly inflated, rounded.

Generally a dark brownish black species with distal parts of legs yellowish brown; wings yellowish brown with periphery blackish infumate. Males always with lower face bright yellow, sometimes with genae and fore and mid legs yellow-marked too, and with most of body reddish brown.

**Remarks:** *Thyreodon santarosae* is immediately recognizable by the rather globose, polished and punctate propodeum (Fig. 33), which is quite unlike that of any other Central American *Thyreodon*, although it is similar to the South American species *T. marginipennis* (Brullé). Both species also have a raised quadrate prominence between their antennal sockets (Fig. 15), quite unlike the frons of other species, and have the scutellum rather broad posteriorly. *T. santarosae* differs from *T. marginipennis* in that the carinae flanking the scuto-scutellar groove are simple, rather than strongly anteriorly flattened. The propodeum of *T. marginipennis* bears sparse rugae centrally and anteriorly, although it is otherwise rather like that of *T. santarosae*.

**Biological notes:** *Thyreodon santarosae* is only known to occur in the drier areas of north-western Costa Rica. Only four individuals have been wild-collected but 26 individuals have been reared [84-SRNP-948a; 84-SRNP-1116; 84-SRNP-1124; 84-SRNP-1207; 84-SRNP-1263.1; 84-SRNP-1267; 89-SRNP-283; 91-SRNP-1160; 93-SRNP-2673; 94-SRNP-3669; 95-SRNP-7645; 95-SRNP-10554; 96-SRNP-5780; 96-SRNP-7438; 96-SRNP-7439; 96-SRNP-7448; 96-SRNP-7458; 96-SRNP-7460; 96-SRNP-7465; 96-SRNP-7484; 96-SRNP-7488; 96-SRNP-7815;

96-SRNP-10019; 98-SRNP-12089; 98-SRNP-12187.01; 98-SRNP-12274] (Janzen & Hallwachs, 2003). This wasp (Porter, 1986) has evolutionarily left behind the Spingidae and moved on to the large and naked scoli-bearing (not hairy, not urticating) caterpillars of ceratocampine Saturniidae (Gauld, 1988; Janzen & Gauld, 1997). They are superficially sphingid-like in aspect. This is the only species of *Thyreodon* known to have moved on to Saturniidae (though the structurally similar *T. marginipennis* is an obvious additional candidate; to date the biology of this species is unknown). *T. santarosae* has been reared from all seven species of the medium-sized ACG dry forest Ceratocampinae (*Othorene purpurascens*, *Othorene verana*, *Ptiloscola dargei*, *Syssphinx quadrilineata*, *Syssphinx mexicana*, *Syssphinx molina*, *Syssphinx colla*). It probably does not parasitize the three very large ceratocampine saturniids *Citheronia* and *Eacles* that occur in this habitat, given that 443 of them have been reared without encountering this wasp. The small larva of *Adeloneiva isara*, the single remaining ACG dry forest ceratocampine, may be too small to be an adequate host (32 rearing records, Janzen & Hallwachs, 2003). *T. santarosae* is most easily reared by collecting a large batch of last instar caterpillars of *S. molina* from the crowns of large *Pithecellobium saman* trees. The host caterpillars feed on a variety of species of trees, shrubs and vines in the Fabaceae (Janzen, 2003), except that *O. verana* feeds in the crowns of large oak trees (*Quercus oleioides*, Fagaceae) and *O. purpurascens* feeds in the crowns of large *Manilkara chicle* (Sapotaceae) trees. All of these caterpillars pupate in a depression at the interface of the litter and soil, and the *T. santarosae* cocoons are spun in these depressions. Adult *T. santarosae* search for caterpillars in full daylight, running clumsily over the foliage in the crowns of large trees. Despite its obvious abundance in the ACG dry forest, this wasp has never been caught in 12 trap years of Malaise traps placed in the understory and on forest edges.

This wasp may eclose any time between May and October (during the first two-thirds of the rainy season). Some pupae are dormant for a full year, from June–August through to the following May–June, and are therefore effectively univoltine. Others eclose after only 34–54 days, whereas others remain dormant for 60–100 days. The result is that there can be ovipositing adults in the habitat throughout May–October. During this time there are generally some ceratocampine caterpillars present (especially those of *Syssphinx molina*), though the largest numbers are available in June–July (Janzen, 1993).

**Material examined:** Holotype ♂, COSTA RICA, Guanacaste Prov.: Santa Rosa National Park, 300 m (Janzen & Hallwachs) (USNM).

Non-type material: COSTA RICA: Guanacaste Prov.: 2 ♂, Guanacaste National Park, Finca Jenny, 31 km N Liberia, 240 m, xi.1988, vi.1994 (*Araya*) (INBio); 14 ♀, 12 ♂, Guanacaste National Park, reared as per data listed above (*Janzen & Hallwachs*) (JHVC); 1 ♀, Rincon de la Vieja National Park, Estacion Las Pailas, 800 m, viii–ix.1993 (*Rodriguez & Sihezar*) (INBio); Puntarenas Prov.: 1 ♀, Carara Biological Reserve, Estacion Quebrada Bonita, 50 m, vi.1990 (*Zuñiga*) (INBio).

#### 4. *THYREODON NIGER* CRESSON

*Thyreodon niger* Cresson, 1874: 375. Lectotype ♀, MEXICO: Cordoba, designated by Cresson, 1916: 44 (PANS) [examined].

Fore wing length 22.2 mm; clypeus moderately convex, with apex pointed medially, with extreme apical margin out-flared; malar space about 0.5 times basal mandibular width; maxillary palp long with second palpomere both strongly broadened and flattened; lower face centrally rugose; frons with a pair of very strong vertical crests between antennal sockets and with a sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli small, the lateral ocellus separated from eye by about 1.4 times its own maximum diameter; head in dorsal view with gena rugoso-punctate, rather evenly rounded behind eye, occipital carina strong, its lower end sharp, not reaching hypostomal carina; antenna setaceous, with about 62 flagellomeres, the 20th slightly elongate, 1.1 times as long as broad, the subapical ones with setae which are slightly shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, centrally impressed ridge which is separated from the anterior margin by a deep U-shaped groove; epomia present on upper part of pronotum as a keel extending under anterior reflexed margin; propleuron sparsely punctate, with lower corner unspecialized; mesoscutum sparsely but coarsely punctate, with broad, reticulated notauli that are confluent posteriorly, inner anterior margin of notaulus forming a sharp longitudinal crest; scuto-scutellar groove very deep, laterally margined by very strongly raised carinae; scutellum coarsely punctate, convex; mesopleuron moderately closely punctate, without a sternular impression; metapleuron finely and closely punctate, with a few diagonal striae; propodeum laterally flattened, finely rugose/striate, abruptly rounded above and behind the spiracle, with a weak ridge; propodeum posterodorsally finely rugose-reticulate, with a few sublongitudinal rugae posterolaterally, centrally with a single broad shallow longitudinal impression. Fore leg rather stout, with

coxa with a bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 0.9 times as long as preceding two tarsomeres, with tarsal claw long and with fine close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 6.5 times as long as maximally deep; hind tarsus of male with moderately long, dense pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.9 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly slightly laterally compressed; tergite II+ missing. Male with subgenital plate small and convex, covered with fine hairs; claspers quite long, the dorsal apex obliquely truncate, the lower margin angled before apex, and with a shallow, broad dorsal notch; aedeagus in profile with apex up-turned, weakly inflated, rounded.

A shining black species without a noticeable metallic reflection; wings blackish infumate.

*Remarks:* *Thyreodon niger* is rather similar to *T. deansi*, from which it differs in having one rather than three longitudinal grooves on the propodeum, not having a convex, peripherally impressed propleuron, and not having a sternaulus.

*Biological notes:* *Thyreodon niger* is a widespread Mesoamerican species that ranges from northern Mexico south to Costa Rica. In Costa Rica only a single specimen has been collected, and it is one of the two species (out of 23) not yet found in the ACG. Its host is unknown.

*Material examined:* Lectotype ♀, MEXICO: Cordoba (PANS).

Non-type material: COSTA RICA: Puntarenas Prov.: 1 ? sex, Amistad National Park, Estacion Las Mellizas, Fca Cafrosa, 1300 m, x.1989 (*Ramirez & Mora*) (INBio). GUATEMALA: 1 ♀, Alta Verapaz, Cubilguitz (BMNH). MEXICO: Guerrero: 1 ♂, Venta del Zopilote, 900 m (*Smith*) (BMNH); Morelos: 1 ♂, Puente de Ixtla, 1200 m (*Smith*) (BMNH); Tamaulipas: 10 ♀, 4 ♂, nr Ciudad Victoria, ruta 101 W, vi.1975 (*Porter & Weems*) (FSCA).

#### 5. *THYREODON MOROSUS* SMITH

*Thyreodon morosus* Smith, 1879: 230. Holotype ♀, COSTA RICA (BMNH) [examined].

*Thyreodon pulchricornis* Szépligeti, 1906: 133. Lectotype ♀, PERU, designated by Townes & Townes, 1966: 190 (TM) [examined].

Fore wing length 20.7–22.6 mm; clypeus convex, with apex strongly pointed medially and conspicuously flared outwards; malar space about 0.5 times basal mandibular width; maxillary palp long with second



palpomere broadened and flattened; lower face centrally coarsely punctate; frons with a pair of dorsally divergent crests between antennal sockets and with a sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally weakly rugose; ocelli small, the lateral ocellus separated from eye by about 1.3 times its own maximum diameter; head in dorsal view punctate, with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, abruptly in-turned but not reaching hypostomal carina; antenna setaceous, with 58–62 flagellomeres, the 20th slightly transverse, 0.9 times as long as broad, the sub-apical ones with setae which are shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, with a sharp forward projecting ridge which is separated from the anterior margin by a deep U-shaped groove (Fig. 25); epomia weak but discernible on upper part of pronotum; propleuron sparsely punctate, slightly convex, with lower corner flattened but not peripherally impressed; mesoscutum finely punctate, with broad, shallow, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a low, longitudinal ridge; scuto-scutellar groove very deep, laterally margined by a very strongly raised, simple carina; scutellum punctate, convex; mesopleuron moderately closely and rather coarsely punctate, with a shallow sternular impression; metapleuron finely rugose; propodeum laterally slightly flattened, coarsely diagonally striate, with a sharp ridge above and behind the spiracle; propodeum transversely rugose posterolaterally, centrally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa with a bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere about 0.8 times as long as preceding two tarsomeres, with tarsal claw long and with close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with moderately dense, short pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.7–0.8 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 2.6–2.7 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers quite long, the dorsal distal apex obliquely truncate, the lower margin sharply angulate near apex, so apex can appear to have a broadly V-shaped indentation; dorsal margin with a deep median notch, basally slightly expanded (Fig. 59); aedeagus in profile with apex up-turned, weakly inflated, rounded.

A black species with proximal 0.6 or more of flagellum yellowish white; wings uniformly blue-blackish infumate.

*Remarks:* *Thyreodon morosus* closely resembles two sympatric species, *T. erythrocerata* and *T. walkerae*, which are also black with black-tipped yellow-white antennae (Fig. 5). (NB in all these species of *Thyreodon*, the yellow antennae fade to a substantially lighter creamy white colour in museum specimens.) The black-tipped yellow-white antennae alone are sufficient to distinguish these species from all other *Thyreodon* in Costa Rica, but in the past (e.g. Porter, 1984) the three species have been confused under the name *T. morosus*. The true *T. morosus* differs from the other two species in having the propodeum, in lateral view, with very coarse diagonal striae, and having a more or less sharp longitudinal ridge above and behind the spiracle. In the other two species the propodeum is finely reticulate laterally, and there is no trace of longitudinal ridge dorsally (Fig. 29). *T. morosus* also has the mesopleuron more coarsely punctate than do the other species, and the metapleuron is more rugose. The caterpillar host of *T. morosus* is also probably different from that of the other two species (see below).

*Biological notes:* *Thyreodon morosus* is a widespread species that at very least ranges from Costa Rica south to Peru. The few records we have suggest it is primarily found in low- to mid-altitude rain forests. Porter (1984) recorded it from as far north as Yucatan in Mexico, but these records require verification as the species was frequently confused with other taxa, and it does not occur in Costa Rican dry forest with a climate similar to those of Yucatan. It is widely distributed in Costa Rican rain forest. Although this species occurs well within the area of the ACG caterpillar rearing programme, it has not yet been encountered in many thousands of caterpillars and many tens of sphingid species reared from these rain forest sites.

*Material examined:* Holotype ♀, COSTA RICA, Cartago Prov., Cachí (Rogers) (BMNH). Lectotype ♀, (*T. pulchricornis*) PERU, Marcapata, 1000 m (TM).

Non-type material: COSTA RICA: Guanacaste Prov.: 1 ♀, Guanacaste National Park, Estacion Cacao [= Mengo], 1000 m, vi.1987 (Janzen) (BMNH); 3 ♂, Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, iii–iv.1989 (Biodiversity Survey) (INBio); 1 ♂, Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, ix.1991 (Rios) (INBio): Puntarenas Prov.: 1 ♀, Monteverde, Estacion Brenes, 1300 m, vi.1991 (Bello) (INBio); 2 ♀, Monteverde, San Luis, 1040 m, ix–x.1992 (Fuentes & Quesada) (INBio); 1 ♀, Osa Peninsula, Corcovado National Park, 10–100 m, iii.1982 (Janzen & Hallwachs) (INBio); 1 ♂,

Osa Peninsula, Rancho Quemado, 200 m, xii.1991 (*Quesada*) (INBio); 1 ♂, Sitio Tinieblas, 2 km NE de la Tigra, 1440 m, v.1996 (*Navarro*) (INBio).

#### 6. *THYREODON LATICINCTUS* CRESSON

*Thyreodon laticinctus* Cresson, 1874: 376. Holotype ♀, MEXICO (PANS) [examined].

*Thyreodon principalis* Smith, 1879: 230. Holotype ♀, COSTA RICA (BMNH) [examined].

*Thyreodon zonatus* Szépligeti, 1906: 134. Lectotype ♂, BOLIVIA, designated by Townes & Townes, 1966: 189 (TM) [examined].

*Oleter selenaction* Shestakov, 1926: 259. Lectotype ♀, 'Nova Grenada', designated by Townes & Townes, 1966: 189 (ZISP).

Fore wing length 21.2–22.8 mm; clypeus convex, with apex strongly pointed medially; malar space about 0.5 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and flattened; lower face centrally punctate with a few distinct rugae; frons with a pair of dorsally divergent crests between antennal sockets and with a low but sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli small, the lateral ocellus separated from eye by about 1.3 times its own maximum diameter; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, abruptly in-turned but not reaching hypostomal carina; antenna setaceous, with 51–55 flagellomeres, the 20th slightly transverse, 0.8–0.9 times as long as broad, the subapical flagellomeres with setae that are slightly longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, quadrate ridge which is separated from the anterior margin by a deep U-shaped groove (Fig. 22); epomia weak but discernible on upper part of pronotum; propleuron sparsely punctate, with lower corner rounded, peripherally not impressed; mesoscutum finely punctate, with broad, shallow, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a low, sharp ridge; scuto-scutellar groove very deep, long, laterally margined by very strongly raised, thickened, simple carinae; scutellum rugose-punctate, convex; mesopleuron finely to moderately closely punctate, without a sharp sternal impression; metapleuron finely punctate with a few obscure diagonal ridges; propodeum laterally slightly flattened, finely rugose, with a sharp (and often rather smooth) low ridge above and behind the spiracle; propodeum posterodorsally finely rugose, with stronger transverse rugae posterolaterally, cen-

trally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa with a bluntly rounded protuberance behind trochanteral insertion; 5th tarsomere subequal in length to preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.85–1.00 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 2.2–2.5 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers quite long, the dorsal apex usually produced into a moderately long spine-like projection, the lower margin quite sharply angulate before apex (Fig. 56); aedeagus in profile with apex up-turned, weakly inflated, rounded.

A black species with tergite III and most of tergite IV bright lemon-yellow; wings uniformly blackish infumate.

*Remarks:* *Thyreodon laticinctus* is most easily distinguished by its very striking colour pattern (Fig. 4), being entirely black except for tergites III and IV, which are bright lemon-yellow. In Costa Rica only one other species has a similar colour pattern, *T. whitfieldi*. These two species are extremely similar and have been confused in all collections to date. However, they differ subtly but consistently. *T. laticinctus* has the propodeum with a low, sharp (and often polished) ridge above and behind the spiracle, has tergite II (Fig. 20), in lateral view, 2.2–2.5 times as long as posteriorly deep, has a slightly rugose central region on the lower face, and has the hind femur slender about 6 times as long as deep. *T. whitfieldi* has the propodeum with the upper anterior part evenly convexly rounded, without a sharp ridge above and behind the spiracle (Fig. 19), has tergite II, in lateral view, 1.6–2.0 times as long as posteriorly deep, has the lower face centrally regularly closely and coarsely punctate, and has the hind femur slightly stouter. Only *T. laticinctus* has been reared from *Xylophanes anubus*, again emphasizing its distinctness from *T. whitfieldi*, which has been reared from *Xylophanes chiron*.

*Biological notes:* *Thyreodon laticinctus* is a rather common and widespread species that has a range extending from tropical Mexico south to Bolivia (though again, as in other cases, it may be that many museum specimens of '*T. laticinctus*' are *T. whitfieldi* or yet other species). Both *Thyreodon laticinctus* and *Thyreodon whitfieldi* (the two are indistinguishable in

flight) are occasionally encountered flying 50–150 cm above the ground through the understorey of relatively intact Costa Rican rain forest, lower elevation cloud forest and their intergrades, during full daylight and in bright sunlight. Their conspicuousness (black and yellow), abundance and slow flight are reflected in the large number of specimens of both species (and both sexes) in the INBio collections. Neither species has ever been encountered in classical Guanacaste Province dry forest (the two wild-caught records of *T. laticinctus* from Cerro El Hacha and the rearing records from the western lower slopes of Volcán Orosi are from an ACG forest type that is in the moist intergrade between classical lowland dry forest and bordering rain forest). *T. laticinctus* does not come to lights and is almost never caught in Malaise traps.

*Thyreodon laticinctus* has a wider geographical distribution in Costa Rica than does *Thyreodon whitfieldi*, with the latter species apparently restricted to the intermediate to upper elevation areas (600–1000 m) of the ACG.

*Thyreodon laticinctus* is unambiguously a specialist on caterpillars of *Xylophanes anubus* (Sphingidae) feeding on various species of *Psychotria* (Rubiaceae), a common member of the rain forest understorey (all rearing records [98-SRNP-13527; 98-SRNP-14002; 98-SRNP-14139; 99-SRNP-698; 99-SRNP-873; 99-SRNP-8959; 99-SRNP-8969; 99-SRNP-12437; 00-SRNP-789; 00-SRNP-1289] are from this caterpillar species; Table 1). This wasp occurs at a very low density. Of 382 *Xylophanes anubus* caterpillars found in the habitats where it has been reared, only ten (2.6%) were attacked. The strong host-specificity of *T. laticinctus* is particularly dramatic when it is considered that along with the *Xylophanes anubus* caterpillars collected were another 800 *Xylophanes* caterpillars of 11 different species, 512 of which were found feeding on *Psychotria* spp.

Oviposition may occur as early as ante-penultimate (3rd) instars. The larva exits the prepupal caterpillar cadaver in the pupal chamber made of leaves and a few strands of silk in the litter. The tough strong wasp cocoon is spun in the caterpillar's pupal chamber. The adult wasp cuts its way out of the cocoon 32–283 days later (see rearing records in Janzen & Hallwachs, 2003), and during just about any month. This apparent variable multivoltinism is congruent with the fact that *Xylophanes anubus* caterpillars may be found in just about any month of the year (though in highly variable numbers) in the rain forests and cloud forests occupied by the portion of the *X. anubus* population used by *T. laticinctus* (in the ACG dry forest, *X. anubus* caterpillars are present only during the first 4–5 months of the 6-month rainy season). The wild-caught records of *T. laticinctus* suggest a flight period throughout the year, just as do the rearing records.

*T. laticinctus* offers a particularly good example of a parasitic wasp that does not occupy all of its host's geographical range. *Xylophanes anubus* caterpillars are found feeding on *Psychotria* spp. throughout the understorey of ACG rain forest, lower cloud forest and dry forest. They are particularly abundant in ACG dry forest during the first 3 months of the rainy season. These dry forests range from 0 to 30 km distant from the wetter rain forests where adult *T. laticinctus* have been caught frequently and the ten parasitized caterpillars were found. However, no species of *Thyreodon* has been reared from the 490 wild-caught *X. anubus* caterpillars found in the ACG dry forests up until 2002, even though these were collected during rainy season months (Janzen & Hallwachs, 2003), a time when the forest understorey in dry forest and adjacent wetter forests seem microclimatologically to be very similar. *T. laticinctus* is restricted to rain forest by factors other than simple presence of its host caterpillar.

*Material examined:* Holotype ♀, (*T. laticinctus* Cresson) MEXICO, Orizaba (PANS); Holotype ♀, (*T. principalis* Smith) COSTA RICA, Cartago Prov., Cachí (BMNH); lectotype ♂, (*Thyreodon zonatus* Szépligeti) BOLIVIA, Juntas (TM).

Non-type material: BELIZE: 1 ♀, Punta Gorda (BMNH). COSTA RICA: Alajuela Prov.: 2 ♀, Falda Este, Volcán Tenorio, Colonia Río Celeste, Finca Magli, 400–500 m, xi.1988 (*Solis*) (INBio); 3 ♀, same locality, iv.1988 (*Soto*) (UCRC); 1 ♀, Finca San Gabriel, 2 km W Dos Rios, 600 m, v.1990 (*Parataxonomists*) (INBio); 2 ♀, San Ramon, Río San Lorencito, 800–850 m, iv–v.1987 (*Solis*) (INBio); 2 ♀, San Ramon Biological Reserve, 800 m, I–iii.1995 (*Carballo*) (INBio); 2 ♀, 2 ♂, Sector Colonia Palmareña, 9 km SW Bajo Rodriguez, 700 m, ix.1995, iv.1997 (*Saborio & Carballo*) (INBio); 7 ♀, 2 ♂, Sector San Ramon, 620 m, iv.1994 (*Parataxonomists*) (INBio); 2 ♀, Zapote, Upala, iii.1988 (*Chacon*) (INBio); Cartago Prov.: 1 ♂, Turrialba (USNM); 1 ♂, Volcán Irazú, 2–2200 m (*Rodgers*) (BMNH); Guanacaste Prov.: 1 ♀, 1 ♂, Guanacaste National Park, Cerro el Hacha, 400 m, v.1988 (*Espinoza*) (INBio); 2 ♀, 1 ♂, Guanacaste National Park, Estacion Pitilla, 680 m, xi.1988, v.1989, i.1991 (*Gauld & Mitchell*) (BMNH); 50 ♀, 16 ♂, Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, vii.1988, vii.1991, iii–v, ix–x.1992, iv.1994 (*Parataxonomists*) (INBio); 3 ♀, Guanacaste National Park, Estacion Pitilla, Finca Pasmompa, 5 km SW Sta Cecilia, 400 m, iii.1989 (*Parataxonomists*) (INBio); 1 ♀, Guanacaste National Park, Estacion Cacao, 1000–1400 m, xii.1989, vi.1990 (*Gudamuz*) (INBio); 1 ♀, Guanacaste National Park, Estacion Maritza, 700 m, vi.1986 (*Gauld*) (BMNH); 9 ♀, 2 ♂, Guanacaste National Park, reared as per data listed above (*Janzen & Hallwachs*) (JHVC); 1 ♀, Rincon de la Vieja



National Park, Las Pailas, 800 m, iii.1993 (*Parataxonomists*) (INBio); 2 ♀, Rincon de la Vieja National Park, Las Pailas, 800 m, v.1994 (*Taylor*) (INBio); Heredia Prov.: 2 ♀, Braulio Carrillo National Park, Estacion El Ceibo, 400–600 m, x.1989 (*Parataxonomists*) (INBio); 1 ♀, La Selva Biological Station, 50–150 m, iii.1988 (*Soto*) (UCRC); Limón Prov.: 1 ♀, Guapiles (*Schaus*) (USNM); Puntarenas Prov.: 4 ♀, Amistad National Park, Finca Cafrosa, Las Mellizas, 1300 m, iii, vi.1991 (*Ramirez*) (INBio); 1 ♀, same locality, iv.1996 (*Chinchilla*) (INBio); 1 ♀, Monteverde Reserve, San Luis, Buen Amigo, 1350 m, v.1994 (*Fuentes*) (INBio); 1 ♀, 1.4 km NE La Tigra, Avenida el Pizote, 1300 m, viii.1996 (*Navarro*) (INBio); San José Prov.: 2 ♀, Braulio Carrillo National Park, Estacion Carrillo, 700 m, ii.1993 (*Parataxonomists*) (INBio). GUATEMALA: 1 ♂, Vera Paz, Senahu (*Champion*) (BMNH); 1 ♀, Zapote (*Champion*) (BMNH). PANAMA: 1 ♂, Cerro Campana, vii.1970 (*Howden*) (AEIC). We have also seen specimens from Colombia, Ecuador and Peru (in AEIC, BMNH).

#### 7. *THYREODON WHITFIELDI* GAULD SP. NOV.

Fore wing length 21.5–24.0 mm; clypeus weakly convex, with apex flared outwards, strongly pointed medially; malar space about 0.5 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and flattened; lower face centrally regularly coarsely and closely punctate; frons with a pair of dorsally divergent crests between antennal sockets and with a low but sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli small, the lateral ocellus separated from eye by about 1.4–1.5 times its own maximum diameter; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, abruptly in-turned but not reaching hypostomal carina; antenna setaceous, with 62–68 flagellomeres, the 20th slightly transverse, 0.6–0.7 times as long as broad, the subapical flagellomeres with setae that are shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, quadrate ridge which is separated from the anterior margin by a deep U-shaped groove (Fig. 21); epomia weak but discernible on upper part of pronotum; propleuron sparsely punctate, with lower corner rounded, peripherally weakly impressed; mesoscutum punctate, with broad, shallow, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a moderately high, sharp ridge; scuto-scutellar groove very deep, long, laterally margined by very strongly raised carinae; scutellum closely punctate,

convex; mesopleuron moderately closely punctate, with a slightly more coarsely sculptured diagonal band from lower hind corner to near upper end of epicnemial carina, without a sharp sternal impression; metapleuron finely punctate with weak diagonal ridges; propodeum laterally slightly flattened, finely rugose, with upper anterior part convexly rounded, without any trace of a sharp ridge above and behind spiracle; propodeum posterodorsally finely rugose, with stronger transverse rugae posterolaterally, centrally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa slightly flattened with a low bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 1.2–1.3 times as long as the preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur quite stout, about 5 times as long as maximally deep; hind tarsus of male with dense, unusually long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.9–1.0 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 1.6–2.0 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers of moderate length, the dorsal apex produced into a short spine-like projection, the lower margin barely angulate before apex (Fig. 55); aedeagus in profile with apex up-turned, strongly inflated, rounded.

A black species with tergites III and most of IV bright lemon-yellow; wings uniformly blackish infumate.

*Remarks:* *Thyreodon whitfieldi* is named in honour of James B. Whitfield, in recognition of his identification of tens of thousands of tiny black microgastrine braconid wasps reared by the ACG caterpillar inventory. *T. whitfieldi* is most easily distinguished from most *Thyreodon* species by its very striking colour pattern, being entirely black except for tergites III and IV, which are bright lemon-yellow. In Costa Rica only one other species has a similar colour pattern, and this is *T. laticinctus*. These two species are extremely similar and have been confused in all collections to date, as well as when it is seen flying. However, they differ subtly but consistently. *T. whitfieldi* has the propodeum with the upper anterior part evenly convexly rounded, without any trace of a sharp ridge above and behind the spiracle, has tergite II, in lateral view, 1.6–2.0 times as long as posteriorly deep, and has the hind femur stouter. *T. laticinctus* has the propodeum with a low, sharp (and often polished) ridge above and behind the spiracle, has tergite II, in lateral view,

2.2–2.5 times as long as posteriorly deep, and has the hind femur slender, about 6 times as long as deep. They also differ in the form of the antennae of the female. Those of *T. whitfieldi* have consistently more flagellomeres (63–68) than do those of *T. laticinctus* (51–55), have the central flagellomeres more transverse (0.6–0.7 times as long as broad) and the apical ones with shorter setae. The apical flagellomeres of *T. laticinctus* have setae that are longer than the diameter of the flagellomere. The apex of the aedeagus of *T. whitfieldi* is much stouter and more rounded than that of *T. laticinctus*, and the dense pubescence on the hind tarsus is slightly longer and more conspicuous.

*Biological notes:* *Thyreodon whitfieldi* is only known to occur in the ACG. Individuals have been collected in a wide range of rain forest and cloud forest between about 500 and 1400 m. Although this species occurs well within the area of the ACG caterpillar rearing programme, it has only been reared on a single occasion. A single female has been reared in Rincon rain forest from the larva of *Xylophanes chiron* Drury found feeding on *Psychotria berteriana* (Rubiaceae) [02-SRNP-21531]. The larva was collected in December, and the ichneumonid emerged from its cocoon the following March. Rearing 285 other specimens of *X. chiron* did not produce any other specimens of *Thyreodon*.

*Material examined:* Holotype ♀, COSTA RICA, Guanacaste Prov., Guanacaste National Park, Estacion Cacao, SW side of Volcán Cacao, 1000–1400 m, v–vi.1991 (*Parataxonomists*) (INBio). Paratypes: COSTA RICA: Alajuela Prov.: 1 ♀, Finca 6, Rincon rain forest, ACG, reared, data given above (*Perez*) (JHVC); 1 ♀, Sector San Ramon de Dos Rios, 620 m, iv–v.1996 (*Quesada*) (INBio); Guanacaste Prov.: 5 ♀, 1 ♂, Guanacaste National Park, Estacion Maritza, on W side Volcán Orosi, 560 m, v, x.1988, iv–vi.1989 (*Gauld & Mitchell*) (BMNH); 1 ♂, Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, iii.1990 (*Rios, Moraga & Blanco*) (INBio); 3 ♀, Guanacaste National Park, Estacion Cacao, 1000–1400 m, iii–viii.1990, v–vi.1991 (*Parataxonomists*) (INBio); 1 ♀, Guanacaste National Park, Estacion Cacao, Arenales, 1100 m, vi.1990 (*Parataxonomists*) (INBio); 1 ♀, Hda Santa Maria, 750 m (INBio) (INBio); 7 ♀, 1 ♂, Rincon de la Vieja National Park, Las Pailas, 800 m, viii–ix.1992, vii, x.1993, iv, vi.1994 (*Garcia*) (INBio); 2 ♀, same locality, 4 km S Cerro Braun, 1100 m, iv–v.1996 (*Masis & Espinoza*) (INBio); 1 ♀, same locality, 2.5 km S Cerro Braun, 1250 m, iv.1996 (*Masis*) (INBio); 1 ♀, same locality, 2 km S Cerro Braun, 1000–1400 m, vii.1996 (*Ugalde*) (INBio); 1 ♀, Rincon de la Vieja National Park, Las Pailas, 800 m, iv.1994 (*Taylor*) (INBio).

#### 8. *THYREODON DEANSI* GAULD SP. NOV.

Fore wing length 16.5–17.8 mm; clypeus weakly convex, with apex bluntly pointed medially, with extreme apical margin rather abruptly out-turned; malar space about 0.6 times basal mandibular width; maxillary palp long with second palpomere both strongly broadened and flattened; lower face centrally sparsely but moderately coarsely punctate; frons with a pair of strong vertical crests between antennal sockets and with a sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli small, the lateral ocellus separated from eye by about 1.6–1.7 times its own maximum diameter; head in dorsal view with gena coarsely punctate, rather evenly rounded behind eye, occipital carina strong, its lower end sharp, not reaching hypostomal carina; antenna setaceous, with about 61 flagellomeres, the 20th slightly transverse, 0.8–0.9 times as long as broad, the subapical ones with setae which are slightly shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, centrally impressed ridge which is separated from the anterior margin by a deep U-shaped groove; epomia present on upper part of pronotum as a keel extending under anterior reflexed margin; propleuron sparsely punctate, with lower corner convex, expanded slightly to form a lobe which peripherally is shallowly impressed and bears a few weak rugae; mesoscutum sparsely but coarsely punctate, with broad, moderately shallow, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a high, sharp transverse crest; scuto-scutellar groove very deep, laterally margined by very strongly raised carinae; scutellum punctate, convex; mesopleuron moderately closely punctate, with a sharp, deep, complete sternaular impression; metapleuron finely and closely punctate; propodeum laterally flattened, finely reticulate, abruptly rounded above and behind the spiracle, but without a distinct ridge; propodeum posterodorsally finely reticulate, with a few transverse rugae posterolaterally, centrally with a broad fairly deep longitudinal impression, laterally flattened with a weak to moderate lateromedian longitudinal impression. Fore leg of female rather stout, with coxa with a bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 1.1–1.2 times as long as preceding two tarsomeres, with tarsal claw unusually long and with inner pectinae separated from outer pectinae by a short gap; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore

wing with abscissa of *Cu1a* between *Cu1b* and *2m-cu* 0.9–1.0 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 2.9–3.2 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers long, the dorsal apex produced into a long spine-like projection, the lower margin not angulate before apex; aedeagus in profile with apex up-turned, weakly inflated, rounded.

A shining black species without a noticeable metallic reflection; wings of female uniformly blackish infumate. Male, similar in colour, but with antennae, facial orbits and fore leg yellowish marked, wings strongly yellowish infumate.

*Remarks:* *Thyreodon deansi* is named in honour of Andrew R. Deans, in recognition of his identification of thousands of slightly larger black microgastrine braconid wasps reared by the ACG caterpillar inventory. Although the male differs from the two females in colour, we are reasonably certain it is conspecific as both share a number of unusual features, including the slightly inflated, and peripherally impressed propleuron, and the sharply impressed sternaular groove. These two features distinguish *T. deansi* from the rather similar *T. apricus*, which also has three longitudinal grooves on the propodeum.

*Biological notes:* *Thyreodon deansi* is only known to occur in Costa Rica. It has only been collected three times, twice in the ACG and once on the Osa Peninsula. Although this species occurs well within the area of the ACG caterpillar rearing programme, it has not yet been encountered in many thousands of caterpillars and many tens of species of sphingids reared from these rain forest sites.

*Material examined:* Holotype ♀, COSTA RICA, Guanacaste Prov., Guanacaste National Park, Estacion Pitilla, 9 km S Santa Cecilia, 700 m, v.1990 (*Biodiversity Survey*) (INBio). Paratypes: COSTA RICA: Guanacaste Prov.: 1 ♀, Guanacaste National Park, Estacion Cacao, 1000–1400 m, x.1989 (*Blanco & Chavez*) (INBio); Puntarenas Prov.: 1 ♂, Osa Peninsula, Corcovado National Park, Estacion Sirena, 1–100 m, ix.1993 (*Fonseca*) (INBio).

#### 9. *THYREODON APRICUS* PORTER

[*Thyreodon niger* Cresson; Porter 1976: 306. Misidentification, in part.]

*Thyreodon apricus* Porter, 1984: 57. Holotype ♂, MEXICO (FSCA) [examined].

Fore wing length 17.9–20.4 mm; clypeus weakly convex, with apex bluntly pointed medially; malar space 0.5–0.6 times basal mandibular width; maxillary palp

long with second palpomere both strongly broadened and flattened; lower face centrally punctate with weak coriaceous sculpture; frons with a raised area between antennal sockets but without distinct vertical crests; frons with a sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli small, the lateral ocellus separated from eye by about 1.3–1.4 times its own maximum diameter; head in dorsal view with gena finely punctate, rather evenly rounded behind eye, occipital carina strong, its lower end sharp, not reaching hypostomal carina; antenna setaceous, with about 54 flagellomeres, the 20th slightly transverse, 0.8–0.9 times as long as broad, the subapical ones with setae which are slightly shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, centrally impressed ridge which is separated from the anterior margin by a deep U-shaped groove; epomia present on upper part of pronotum as a weak keel extending under anterior reflexed margin; propleuron sparsely punctate, with lower corner flat, peripherally weakly rugulose; mesoscutum sparsely but coarsely punctate, with broad, moderately deep, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a sharp transverse crest; scuto-scutellar groove very deep, laterally margined by a very strongly raised carina that is laterally slightly expanded; scutellum finely punctate, convex; mesopleuron polished and very sparsely punctate, without a sternaular impression; metapleuron transversely rugose; propodeum laterally flattened, finely reticulate/rugose, abruptly rounded above and behind the spiracle, with an indistinct ridge; propodeum posterodorsally finely reticulate, with transverse rugae posterolaterally, centrally with a broad fairly deep longitudinal impression, laterally flattened with a weak to moderate lateromedian longitudinal impression. Fore leg of female stout, with coxa with a large, bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 0.7–0.8 times as long as preceding two tarsomeres, with tarsal claw long and closely pectinate; hind coxa in profile small, its hind end not quite reaching level of hind end of propodeum; hind femur stout, about 4.5–5.0 times as long as maximally deep; hind tarsus of male with very long coarse, sparse pubescence ventrally. Fore wing with abscissa of *Cu1a* between *Cu1b* and *2m-cu* 0.7–0.8 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 2.1–2.2 times as long as posteriorly deep. Male with subgenital plate small and rather flat, covered with coarse hair; claspers long, the dorsal apex pro-



duced into a spine-like projection, the lower margin not angulate before apex; aedeagus in profile slender, with apex simply up-turned.

A shining black species without a noticeable metallic reflection; flagellum blackish brown, lighter in ♂ wings uniformly blue-blackish.

*Remarks:* *Thyreodon apricus* superficially closely resembles *T. deansi*, which also is non-metallic black and has three longitudinal grooves on the propodeum. However, the two species differ in many features. *T. apricus* lacks the strong frontal crests present in *T. deansi*, and has the vertex more finely punctate. *T. apricus* also has the metapleuron transversely rugose rather than finely closely punctate, and it lacks the gap in the pecten of the fore tarsal claws. The males differ in that *T. apricus* has very long sparse pubescence on the hind tarsus, whereas that of *T. deansi* is much shorter and denser.

*Biological notes:* *Thyreodon apricus* is a widespread Mesoamerican species that ranges from the southern part of Texas, southwards to north-western Costa Rica. It seems to be restricted to areas with a strong dry season. Porter (1984) remarks that he collected this species in Texas under sparse *Acacia*, in *Celtis* woodlands and around *Prosopis* and *Pithecellobium* groves. This species has been reared only once by the ACG caterpillar and parasitoid inventory [87-SRNP-1319], from a last instar larva of *Erinnyis lassauxii* (Sphingidae) feeding on *Macrosepiis obovata* (Asclepiadaceae). A second caterpillar of the same species produced an identical *Thyreodon* cocoon but the wasp died without developing. Both records are from the ACG dry forest (Janzen & Hallwachs, 2003). The parasitoid larva killed its host in the pupation retreat, then spun a cocoon from which the adult wasp emerged about 1 month later.

As more than 15 000 other sphingid larvae (including 1400+ members of the genus *Erinnyis*) of about 65 species (including six species of *Erinnyis*) have been reared from the ACG dry forest, we feel comfortable in concluding that *Erinnyis lassauxii* is probably the sole species attacked by *T. apricus*. *E. lassauxii*, with a range from the south-western USA to Argentina (D'Abrera, 1986), easily covers the dry forest geographical and ecological range of *T. apricus*.

*Material examined:* Holotype ♂, MEXICO, Mexico, Chalma, vi.1974 (Porter) (FSCA). Paratypes: HONDURAS: 1 ♀, Puerto Castillo, iii.1924 (USNM). MEXICO: Chiapas: 1 ♀, Cachuatil, c. 50 km SW Cintalapa, 500–700 m, viii.1965 (Weems) (FSCA): Tamaulipas: 2 ♂, nr San Antonio on ruta 101, vi.1982 (Porter) (FSCA). USA: Texas: 2 ♀, Hidalgo Co., Bentsen Rio Grande Valley State Park, iii–v.1977 (Porter) (FSCA).

Non-type material: COSTA RICA: Guanacaste Prov.: 1 ♀, Guanacaste National Park, Finca Jenny, 31 km N Liberia, 240 m, vi.1994 (Araya) (INBio); 1 ♀, Guanacaste National Park, reared as per data above (Janzen & Hallwachs) (JHVC); 1 ♀, Guanacaste National Park, Estacion Los Almendros, 300 m, vi.1995 (Lopez) (INBio); 1 ♀, 1 ♂, Santa Rosa National Park, 300 m, vi.1985 (Janzen & Gauld) (BMNH); 1 ♀, same locality, 300 m, vi.1992 (Parataxonomists) (INBio); 1 ♀, 1 ♂, same locality, 300 m, vi.1992 (Pereira) (INBio).

#### 10. *THYREODON WALKERAE* GAULD SP. NOV.

Fore wing length 19.9–20.5 mm; clypeus convex, with apex strongly pointed medially and conspicuously flared outwards; malar space 0.4–0.5 times basal mandibular width; maxillary palp long with second palpomere broadened and flattened; lower face centrally coriaceous to slightly rugose; frons with a pair of dorsally divergent crests between antennal sockets and with a sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally weakly rugose; ocelli small, the lateral ocellus separated from eye by about 1.3 times its own maximum diameter; head in dorsal view punctate, with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, abruptly in-turned but not reaching hypostomal carina; antenna setaceous, with 58–60 flagellomeres, the 20th slightly transverse, 0.9 times as long as broad, the subapical ones with setae which are shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming a blunt angular ridge which is separated from the anterior margin by a deep U-shaped groove (Fig. 26); epomia weak but discernible on upper part of pronotum; propleuron sparsely punctate, slightly convex, with lower corner flattened but not peripherally impressed; mesoscutum finely punctate, with broad, shallow, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a sharp, high, transverse crest (Fig. 38); scuto-scutellar groove very deep, laterally margined by a very strongly raised, simple carina; scutellum with close, fine punctures, convex; mesopleuron finely and sparsely punctate, with a shallow sternal impression; metapleuron finely punctate with a few ridges anteriorly; propodeum laterally weakly flattened, quite finely reticulate, rounded and without a ridge above and behind the spiracle; propodeum posterodorsally reticulate, centrally with a single longitudinal impression. Fore leg of female rather stout, with coxa with a bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere about 0.9 times as long as preceding two tarsomeres, with tarsal claw long and with close pectinae; hind coxa in profile

moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with moderately dense, coarse, long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.7–0.8 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly subcylindrical; tergite II, in lateral view, 2.6–2.7 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers quite long, the dorsal distal apex obliquely truncate, the lower margin slightly angulate near apex, but with apex without a broadly V-shaped indentation; dorsal margin with a deep median notch, basally slightly expanded; aedeagus in profile slender, with apex expanded, rounded on extreme apex, with a weak lateral keel.

A black species with proximal 0.6 or more of flagellum yellow-whitish; wings uniformly brownish black infumate.

*Remarks:* *Thyreodon walkerae* is named in honour of Annette K. Walker, in recognition of her identification of thousands of *Microplitis* wasplets (Braconidae) reared by the ACG caterpillar inventory. *Thyreodon walkerae* closely resembles two sympatric species, *T. morosus* and *T. erythrocer*a, which are also black with black-tipped yellow-white antennae. It differs from *T. morosus* in having the propodeum, in lateral view, reticulate, and without a longitudinal ridge above and behind the propodeal spiracle. Unlike *T. erythrocer*a, which has the anterior part of the notaulus more or less flat, *T. walkerae* has a pronounced transverse mesoscutal crest. It also differs from *T. erythrocer*a in having the lower face coriaceous to rugose, rather than coarsely punctate, and in having the posterior ridge of the pronotum quadrate in profile, not overhanging the transverse groove.

*Biological notes:* *Thyreodon walkerae* is only known to occur in Costa Rica. Almost all individuals were collected or reared in the forest on Volcán Cacao in Sector Cacao of the ACG, although one adult has been taken on the Caribbean side of the country in Limón Province. *T. walkerae* has been reared on 60 occasions (Table 1) from the larvae of *Xylophanes hannemanni* feeding on species of Rubiaceae, notably *Coussarea austin-smithii* (ten), *Psychotria panamensis* (nine), *Psychotria* sp. (six), *Palicourea padifolia* (six), *Psychotria correae* (five) and *Psychotria eurycarpa* (four) [96-SRNP-7049; 97-SRNP-1184; 97-SRNP-1189; 97-SRNP-1190; 97-SRNP-1211; 97-SRNP-1246; 97-SRNP-1276; 97-SRNP-1293; 97-SRNP-1303; 97-SRNP-1304; 97-SRNP-1306; 97-SRNP-1309; 97-SRNP-1348; 97-SRNP-1354; 97-SRNP-1355; 97-SRNP-1380; 97-SRNP-1385; 97-SRNP-1387; 97-SRNP-1400; 97-SRNP-1404.1; 97-SRNP-1419;

97-SRNP-1437; 97-SRNP-1441; 97-SRNP-1449; 97-SRNP-1473; 97-SRNP-1479; 97-SRNP-1512; 97-SRNP-1517; 97-SRNP-1535; 99-SRNP-766; 99-SRNP-852; 99-SRNP-1038; 00-SRNP-9644; 00-SRNP-9663; 00-SRNP-9674; 00-SRNP-9695.01; 00-SRNP-9713; 00-SRNP-9728; 00-SRNP-9731; 00-SRNP-9734; 00-SRNP-9744; 00-SRNP-9748; 00-SRNP-9761; 00-SRNP-9762; 00-SRNP-9791.1; 00-SRNP-9795; 00-SRNP-9808; 00-SRNP-9809; 00-SRNP-9813; 00-SRNP-9836; 00-SRNP-9840; 00-SRNP-9873; 00-SRNP-9876; 00-SRNP-9914; 01-SRNP-6941; 01-SRNP-6968; 01-SRNP-6971; 01-SRNP-6972; 01-SRNP-6973; 01-SRNP-6977]. The parasitoids kill their host as a prepupa and spin a cocoon in late June to early July, and emerge as adults the following year between late April and early June. This species is unambiguously univoltine, and adult wasps are present exactly during the peak availability of *X. hannemanni* caterpillars (which are approximately univoltine, despite their rain forest habitat). *T. walkerae* has never been encountered in more than 5 years of Malaise trapping in the exact forest understorey habitat that is rich in parasitized *X. hannemanni* caterpillars. Adults of what appear to be this wasp have been observed walking and flying clumsily among the understorey foliage during the daytime, apparently searching for host caterpillars.

We view *T. walkerae* as unambiguously a specialist on *T. hannemanni* caterpillars, because it has never been encountered in 370 rearings of 11 other species of *Xylophanes* (and many other sphingids) taken in the same sites (and often the same food plant) as the *T. hannemanni* caterpillars.

*Material examined:* Holotype ♀, COSTA RICA, Guanacaste Prov., Area de Conservacion Guanacaste, Sector Cacao, Sendero Arenales, eclosed 27 June 1998 (Franco) [97-SRNP-1387] (JHVC). Paratypes: COSTA RICA: Guanacaste Prov.: 1 ♀, Guanacaste National Park, Estacion Cacao, 1000–1400 m, v–vi.1990 (Gudamuz) (INBio); 22 ♀, 37 ♂, same locality, reared as per data listed above (Janzen & Hallwachs) (JHVC): Limón Prov.: 1 ♂, Rio Segunda & Rio Banano, 500 m, iv.1985 (Solís) (INBio).

#### 11. *THYREODON ERYTHROCERA* CAMERON

*Thyreodon erythrocer*a Cameron, 1886: 288. Holotype ♀, MEXICO: Yucatan (BMNH) [examined]. [*Thyreodon erythrocer* Cameron; Dalla Torre, 1901: 185. Unjustifiable emendation.]

Fore wing length 21.2–22.8 mm; clypeus convex, with apex strongly pointed medially and conspicuously flared outwards; malar space about 0.5 times basal mandibular width; maxillary palp long with second

palpomere broadened and flattened; lower face centrally coarsely punctate; frons with a pair of dorsally divergent crests between antennal sockets and with a sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally weakly rugose; ocelli small, the lateral ocellus separated from eye by about 1.3 times its own maximum diameter; head in dorsal view punctate, with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, abruptly in-turned but not reaching hypostomal carina; antenna setaceous, with 59–62 flagellomeres, the 20th slightly transverse, 0.9 times as long as broad, the subapical ones with setae which are shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, with a sharp forward projecting ridge which is separated from the anterior margin by a deep U-shaped groove; epomia weak but discernible on upper part of pronotum; propleuron sparsely punctate, slightly convex, with lower corner flattened but not peripherally impressed; mesoscutum finely punctate, with broad, shallow, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a low, longitudinal ridge; scuto-scutellar groove very deep, laterally margined by a very strongly raised, simple carina; scutellum punctate, convex; mesopleuron finely and sparsely punctate, without a sharp sternal impression but with a few isolated foveae; metapleuron finely punctate; propodeum laterally slightly flattened, finely reticulate, rounded and without a ridge above and behind the spiracle; propodeum dorsally reticulate, centrally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa with a bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere about 0.8 times as long as preceding two tarsomeres, with tarsal claw long and with close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with moderately dense, short pubescence ventrally. Fore wing with abscissa of *Cu1a* between *Cu1b* and *2m-cu* 0.7–0.8 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly distinctly laterally compressed; tergite II, in lateral view, 2.6–2.7 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers quite long, the dorsal distal apex simply obliquely truncate (Fig. 54); aedeagus in profile evenly rounded.

A black species with proximal 0.6 or more of flagellum yellowish white; wings uniformly brownish black infumate.

*Remarks:* *Thyreodon erythrocer* closely resembles two sympatric species, *T. morosus* and *T. walkerae*, which are also black with black-tipped yellowish white antennae. It differs from *T. morosus* in having the propodeum, in lateral view, reticulate, and without a longitudinal ridge above and behind the spiracle. Unlike *T. walkerae*, which has a pronounced transverse mesoscutal crest, *T. erythrocer* has the anterior part of the notaulus more or less flat. It also differs from *T. walkerae* in having the lower face coarsely punctate, not coriaceous to rugose.

*Biological notes:* *Thyreodon erythrocer* has been reared only in dry forest, once from *Eupyrrhoglossum sagra* [98-SRNP-9335] among 114 larvae of this species feeding on *Chomelia spinosa* and 27 feeding on *Guettarda macrosperma*, and once from *Aellopos titan* [98-SRNP-5830] out of 1566 caterpillars feeding on *Randia* spp., 35 on *Guettarda macrosperma* and eight on other Rubiaceae (these eight are probably ecological errors for this caterpillar species). *T. erythrocer* either occurs at very low density on these two species of Sphingidae, or its host is some other as yet unsampled species of caterpillar and these two rearing records represent biological errors. It may be noteworthy that both rearing records are from the same year, perhaps representing a year in which this species invaded the dry forest from the neighbouring dry forest–rain forest interface. Its larval–pupal biology appears to be the same as that of other *Thyreodon*. The two reared *T. erythrocer* took 31–38 days from spinning to eclosion, suggesting a rain forest multivoltine biology, despite the two unique dry forest rearing records. However, the holotype is from Yucatan, a region with widespread dry forest.

*Material examined:* Holotype ♀, MEXICO, Yucatan, Valladolid (*Baumer*) (BMNH).

Non-type material: COSTA RICA: Guanacaste Prov.: 2 ♀, Guanacaste National Park, reared as per data listed above (*Janzen & Hallwachs*) (JHVC); 1 ♂, Santa Rosa National Park, 300 m, vii.1992 (*Pereira*) (INBio).

## 12. *THYREODON SHARKEYI* GAULD SP. NOV.

[*Thyreodon erythrocer* Cameron; Porter, 1984: 50. Misidentification.]

[*Thyreodon erythrocer* Cameron; Gauld, 1988: 62. Misidentification.]

Fore wing length 17.2–22.6 mm; clypeus convex, with apex strongly pointed medially; malar space about 0.5 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and flattened; lower face centrally sparsely punctate; frons with a pair of dorsally divergent crests between anten-



nal sockets and with a low but sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli small, the lateral ocellus separated from eye by about 1.2 times its own maximum diameter; head in dorsal view with gena strongly rounded behind eye, occipital carina strong and complete, its lower end reaching hypostomal carina above base of mandible; antenna setaceous, with 55–56 flagellomeres, the 20th slightly transverse, 0.9 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin quadrately swollen, but not projecting as a crest over deep transverse U-shaped groove; epomia more or less absent; propleuron sparsely punctate, with a sharp transverse carina separating off lower corner; mesoscutum closely punctate, with broad, shallow, reticulated notauli which are confluent posteriorly, inner anterior margin of notaulus forming a low, sharp ridge; scuto-scutellar groove very deep, laterally margined by a very strongly broadened carina; scutellum rugose-punctate, convex; mesopleuron finely punctate, without a very shallow, foveolate sternular impression; metapleuron finely punctate with a few obscure diagonal ridges; propodeum laterally slightly flattened, finely reticulate to closely punctate, dorsally rounded, without a ridge above and behind the spiracle; propodeum posterodorsally finely reticulate, centrally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa with a large bluntly rounded protuberance behind trochanteral insertion; 5th tarsomere subequal in length to preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind coxa in profile moderately small, its hind end more or less level with hind end of propodeum, unusual in being more densely pubescent than most other species; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.85 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 1.8–1.9 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense black hair; claspers very long and tapered, the dorsal apex acute, apically obliquely truncate, the lower margin rounded; aedeagus in profile with apex up-turned, weakly inflated, rounded.

A black species with wings blue-blackish infumate. One undersized male is very dark reddish brown.

*Remarks:* *Thyreodon sharkeyi* is named in honour of Michael J. Sharkey, in recognition of his identification

of thousands of large braconid wasps reared by the ACG caterpillar inventory. *T. sharkeyi* has been consistently misidentified as *T. erythrocerca* Cameron. I have re-examined the holotype of *T. erythrocerca*, from Yucatan in Mexico, and conclude that it is not conspecific with other material identified as this species by Porter (1984) and Gauld (1988). After repositioning the palpi of the holotype, which obscured the base of the occipital carina, it is clear that the occipital carina of *T. erythrocerca* is ventrally incomplete and not complete as previously thought. Furthermore, the holotype of *T. erythrocerca* has no trace of a carina on the lower part of the propleuron. *T. sharkeyi* has the lower part of the occipital carina strong and complete to the hypostomal carina, and has a pronounced carina on the lower corner of the propleuron. Like most other species of *Thyreodon*, *T. sharkeyi* has the dorsal posterior part of the propodeum acarinate, but *T. erythrocerca* is distinctive in having a sharp carina laterally, on either side of the petiolar insertion, and diverging anteriorly before fading out about 0.3 of the way along the propodeum.

*Biological notes:* *Thyreodon sharkeyi* is the only large wasp parasitizing the caterpillars of *Xylophanes turbata* in the ACG dry forest (Table 2). It finds them on both of the *X. turbata* food plants (*Hamelia patens* and *Psychotria microdon*, Rubiaceae). [84-SRNP-1045; 88-SRNP-202; 93-SRNP-807.1; 94-SRNP-3074.1; 94-SRNP-3086; 94-SRNP-3090; 94-SRNP-3098; 94-SRNP-3099; 94-SRNP-3108; 97-SRNP-2395; 97-SRNP-2731; 97-SRNP-2751; 97-SRNP-2752; 00-SRNP-7689; 00-SRNP-7891; 00-SRNP-7902.] It was reared from 2.2% of 1000 *X. turbata* caterpillars collected in the third to fifth (last) instars and from none of the 187 caterpillars collected in the first or second instars. *T. sharkeyi* was also reared from 3.3% of 214 third to fifth instar caterpillars of *Xylophanes pluto* feeding on the same two food plants. It was not reared from any of 494 caterpillars of *Xylophanes anubus*, *X. juanita*, *X. tersa*, *X. libya*, *X. ceratomioides*, *X. maculator*, *X. chiron* or *X. porcus* feeding on these same two food plants at the same time in the same place (none of these is parasitized by any other *Thyreodon* in the ACG dry forest). *T. sharkeyi* has not been reared from any of 126 caterpillars of *Xylophanes pluto* feeding on its third usual food plant, *Lindenia rivalis* (Rubiaceae), in the ACG dry forest. We conclude that *T. sharkeyi* is a specialist on *X. turbata* larvae but also takes *X. pluto* larvae when they are feeding on the same food plant as *X. turbata*. It either ignores the eight other species of (equal-sized) *Xylophanes* feeding on the same food plant at the same time, or fails to develop in these eight conspecifics.

*T. sharkeyi* spin the smallest and most slender ovoid cocoons of all the species of *Thyreodon* reared to date.

The cocoons are spun in the caterpillar pupal chamber, which is a nest or basket of litter leaves lightly tacked together with silk.

A single *Cidaphus rostratus* (Ichneumonidae: Mesochorinae) hyperparasite was reared from a presumed *T. sharkeyi* (93-SRNP-1883). The host caterpillar, *X. turbata*, was collected as a third instar on 9 June 1993 while feeding on *Hamelia patens*. The newly eclosed hyperparasite cut an exit hole in the anterior end of the *T. sharkeyi* cocoon on 6 April 1995. This date is 1 month before the beginning of the rainy season and 2 years after spinning its cocoon. During these 2 years, the cocoon was in a dry bottle at ambient temperature inside a non-airconditioned house in the ACG dry forest. Two other cases of this species of hyperparasitoid involved 1–2 years in the cocoon as well (see *Thyreodon rufothorax*).

**Material examined:** Holotype ♀, COSTA RICA, Guanacaste Prov., Santa Rosa National Park, 300 m, vi.1984 (*Janzen & Hallwachs*) (BMNH). Paratypes: COSTA RICA: Guanacaste Prov.: 1 ♀, Santa Rosa National Park, 300 m, vii.1984 (*Janzen & Hallwachs*) (BMNH); 8 ♀, 8 ♂, Guanacaste National Park, reared as per data listed above (*Janzen & Hallwachs*) (JHVC). MEXICO: Nuevo León: 1 ♀, Pedro Iturbide, 32 km W Linares, x.1962 (*Townes*) (AEIC); Sonora: 1 ♀, 1 ♂, Cananca, viii.1974 (*Erickson*) (AEIC); 1 ♀, 'N. Sonora' (*Morrison*) (BMNH).

### 13. *THYREODON ZITANIAE* GAULD SP. NOV.

Fore wing length 22.1–24.5 mm; clypeus convex, with apex strongly pointed medially; malar space about 0.6–0.7 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and slightly flattened; lower face centrally sparsely punctate, slightly rugose below antennal sockets; frons with a weak median vertical ridge between antennal sockets and with a low but sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally finely rugose/striate; ocelli moderately small, the lateral ocellus separated from eye by about 0.8–1.1 times its own maximum diameter; head in dorsal view with gena rather broad, evenly rounded behind eye, occipital carina strong, its lower end sharp, not reaching hypostomal carina; antenna setaceous, with 53–57 flagellomeres, the 20th subquadrate, 1.0–1.1 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, centrally impressed ridge which is separated from the anterior margin by a deep U-shaped groove; epomia weak but discernible on upper

part of pronotum; propleuron very sparsely punctate, with lower corner rounded, not peripherally impressed; mesoscutum finely and sparsely punctate, with narrow, anteriorly shallow notauli which are deeper and more or less confluent posteriorly, inner anterior margin of notaulus unspecialized; scuto-scutellar groove very deep, laterally margined by a very strongly raised, thickened carina; scutellum finely punctate, convex; mesopleuron finely and sparsely punctate ventrally, but with upper part smooth and impunctate, without a sharp sternal impression; metapleuron finely punctate with obscure coriaceous sculpture; propodeum laterally slightly flattened, rugose, with a sharp (and often rather smooth) ridge above and behind the spiracle, and with a distinct zigzag carina extending backwards from this ridge along the lateral margin of the dorsal surface of the propodeum; propodeum posterodorsally finely reticulate, with stronger transverse rugae posterolaterally, centrally with a single broad, shallow, longitudinal impression. Fore leg of female rather stout, with coxa more or less without a rounded protuberance behind trochanteral insertion, with 5th tarsomere 0.5–0.6 times as long as preceding two tarsomeres, with tarsal claw long and with close coarse pectinae; hind coxa in profile moderately large, its hind end projecting slightly behind level of hind end of propodeum; hind femur slender, 6–7 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.2–1.3 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly subcylindrical; tergite II, in lateral view, 2.7–3.2 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with dense coarse black hair; claspers quite long, the dorsal apex obliquely truncate, the upper margin with a deep median notch, the lower margin weakly convex (Fig. 57); aedeagus in profile with apex expanded but flattened on extreme apex, with a very sharp lateral keel.

Head orange-brown, with interocellar area and often part of frons blackish; flagellum black; mesosoma orange-brown; metasoma shining black. Anterior two pairs of legs orange-brown, tarsi blackish; hind legs black; wings uniformly blackish infumate.

**Remarks:** *Thyreodon zitaniae* is named in honour of Nina M. Zitani, in recognition of her enthusiasm for the identification and natural history of *Meteorus* wasps (Braconidae) reared by the ACG caterpillar inventory. *T. zitaniae* is structurally and in colour similar to *T. papei*. Both species have rather small ocelli, and have an orange mesosoma and black metasoma. They differ in several respects, however. *T. zitaniae* has the mesoscutum without any trace of a notaular

crest, has a sharp ridge above and behind the propodeal spiracle, and has the fore wings uniformly black. *T. papei* has a sharp notaular crest on the mesoscutum, has the propodeum rounded above and behind the spiracle, and has a central hyaline area on the fore wing.

**Biological notes:** Although *Thyreodon zitaniae* occurs well within the area of the ACG caterpillar rearing programme, it has not yet been encountered in many thousands of caterpillars and many tens of species of sphingids reared from these low- to mid-elevation rain forest sites.

**Material examined:** Holotype ♀, COSTA RICA, Guanacaste Prov., Guanacaste National Park, Estacion Pitilla, 9 km S Santa Cecilia, 700 m, iv–v.1993 (*Moraga*) (INBio). Paratypes: COSTA RICA: Alajuela Prov.: 1 ♀, 1 ♀, Sector San Ramon, 620 m, iii–iv.1994 (*Taylor & Zumbado*) (INBio); 1 ♀, San Ramon de Dos Rios, 620 m, iv.1995 (*Chinchilla*) (INBio); 1 ♀, 1 ♂, Sector Colonia Palmareña, 700 m, iv.1995, iii.1996 (*Carballo*) (INBio): Guanacaste Prov.: 1 ♀, Guanacaste National Park, Estacion Maritza, 600 m, v.1991 (*Flowers*) (INBio); 4 ♀, Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, viii.1988, iii.1990, ix.1991, iii–v.1993 (*Rios & Moraga*) (INBio): Heredia Prov.: 1 ♀, Braulio Carrillo National Park, Estacion El Ceibo, 400–600 m, iv.1990 (*Chaves*) (INBio); 1 ♂, La Selva Biological Station, 50–150 m, iv.1989 (*Hespenheide*) (BMNH): Puntarenas Prov.: 1 ♀, Amistad National Park, Estacion Las Mellizas, Fca Cafrosa, 1300 m, vi.1991 (*Ramirez*) (INBio).

#### 14. *THYREODON DELVAREI* GAULD SP. NOV.

Fore wing length 18.8–20.5 mm; clypeus weakly convex, with apex flared outwards, bluntly pointed medially; malar space about 0.6 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and slightly inflated; lower face centrally finely and sparsely punctate; frons weakly convex between antennal sockets and without a carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally smooth; ocelli moderately large, the lateral ocellus separated from eye by about 0.7 times its own maximum diameter; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, not reaching hypostomal carina; antenna setaceous, with 50–52 flagellomeres, the 20th subquadrate, 1.0 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, centrally impressed ridge which is separated

from the anterior margin by a deep U-shaped groove; epomia possibly represented on upper part of pronotum by one of several rugae; propleuron smooth, almost impunctate, with lower corner rounded, peripherally not impressed; mesoscutum highly polished, very finely and sparsely punctate, with only a slight vestige of notauli; scuto-scutellar groove very deep, laterally margined by very strongly raised carinae; scutellum polished, finely and sparsely punctate, weakly convex; mesopleuron highly polished, almost impunctate, without a trace of a sternular impression; metapleuron finely punctate; propodeum laterally weakly convex, with a sharp (and often rather smooth) low ridge above and behind the spiracle, rugose with the rugae tending to be parallel lower down; propodeum posterodorsally rugose-reticulate, with strong transverse rugae posterolaterally, centrally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa with a conspicuous bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere about 0.5 of length of preceding two tarsomeres, with tarsal claw moderately long and with moderately coarse, close pectinae; hind coxa in profile moderately large, its hind end extending well beyond hind end of propodeum; hind femur stout, about 4.5–5.0 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 0.9–1.0 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly subcylindrical; tergite II, in lateral view, 2.3–2.5 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with sparse coarse hair; claspers long, the dorsal apex elongately rounded/truncate, slightly inclined upwards without an apical spine-like projection, the lower margin weakly convex; aedeagus in profile with apex up-turned, very weakly flattened, with a sharp lateral keel.

A polished black species with mesopleuron and coxae with a blue-black metallic sheen; wings uniformly blackish infumate.

**Remarks:** *Thyreodon delvarei* is named in honour of Gerard Delvare, in recognition of his enthusiastic identification of the thousands of chalcidid wasps reared by the ACG caterpillar inventory. *T. delvarei* rather closely resembles *T. darlingi* in general appearance and coloration. Both are shining black species with uniformly black wings and a slightly metallic sheen to the mesosoma, both have rather large ocelli, and the males of both species have a long, slightly bent clasper that lacks an apical spine and has the apex of the aedeagus somewhat flattened. *T. delvarei* differs from *T. darlingi* in having slightly smaller ocelli that are separated from the eye margin by about 0.7 of



their own maximum diameter, whereas those of *T. darlingi* are separated by about 0.2 of their maximum diameter. The malar space of *T. delvarei* is wider than *T. darlingi*, it lacks the strongly impressed notauli and it has the mesopleuron much smoother and less sculptured.

*Biological notes:* Although *Thyreodon delvarei* occurs well within the area of the ACG caterpillar rearing programme, it has not yet been encountered in many thousands of caterpillars and many tens of species of sphingids reared from these mid- to upper-elevation rain forest sites.

*Material examined:* Holotype ♀, COSTA RICA, Guanacaste Prov., Rincon de la Vieja National Park, Estacion Las Pailas, 800 m, vi.1992 (*Garcia*) (INBio). Paratypes: COSTA RICA: Guanacaste Prov.: 1 ♀, Guanacaste National Park, Estacion Cacao, 1000–1400 m, vi.1990 (*Parataxonomists*) (INBio): Puntarenas Prov.: 1 ♂, Monteverde, Finca Buen Amigo, 4 km S of Reserve, 1000–1350 m, v.1997 (*Fuentes*) (INBio).

#### 15. *THYREODON SCHAUFFI* GAULD SP. NOV.

Fore wing length 18.0 mm; clypeus convex, with apex pointed medially; malar space 0.5 times basal mandibular width; maxillary palp long with second palpomere very strongly broadened and flattened; lower face centrally finely punctate; frons weakly convex between antennal sockets, unspecialized, with a short sharp carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally more or less smooth; ocelli large, the lateral ocellus separated from eye by about 0.5 times its own maximum diameter; head in dorsal view with gena evenly rounded behind eye, occipital carina strong, its lower end not reaching hypostomal carina; antenna setaceous, with 48 flagellomeres, the 20th elongate, 1.2 times as long as broad, the subapical ones with setae which are shorter than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally quadrately swollen, anteriorly forming an angular projecting ridge which is separated from the anterior margin by a deep U-shaped groove; epomia strong; propleuron extremely sparsely punctate, with lower corner rounded; mesoscutum moderately sparsely punctate, with narrow, deep notauli which are almost confluent posteriorly, inner anterior margin of notaulus unspecialized; scuto-scutellar groove deep, laterally margined by a raised, simple carina; scutellum punctate, convex; mesopleuron smooth and polished, more or less impunctate, without a sternular impression and unusual in lacking lateral part of epicnemial carina; metapleuron finely punctate with a few obscure diagonal ridges peripher-

ally; propodeum laterally weakly flattened, punctate above, with strong diagonal subparallel rugae lower down, with a sharp polished ridge above and behind the spiracle; propodeum posterodorsally with oblique centrally convergent rugae, centrally with a single, shallow, longitudinal impression. Fore leg of female rather slender, with coxa with a bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 0.5 times as long as preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind coxa in profile of moderate size, its hind end projecting beyond level of hind end of propodeum; hind femur slender, about 5 times as long as maximally deep; hind tarsus of male with moderately sparse, short pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.2 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I moderately slender, anteriorly slightly laterally compressed; tergite II, in lateral view, 2.2 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with fine hair; claspers long, the dorsal apex very obliquely truncate, the lower margin rounded before apex; aedeagus in profile with apex up-turned, weakly flattened, with a sharp lateral keel.

An exceptionally highly polished blue-black species with wings uniformly blackish infumate.

*Remarks:* *Thyreodon schauffi* is named in honour of Michael E. Schauff, in recognition of his identification of thousands of *Euplectrus* wasps (Eulophidae) reared by the ACG caterpillar inventory. *Thyreodon schauffi* is immediately recognizable by its highly polished, blue-black integument and because the lateral part of the epicnemial carina is absent, not reaching to the level of the lower corner of the pronotum.

*Biological notes:* *Thyreodon schauffi* is only known from Costa Rica, where only two individuals have been found. An adult female was collected in a Malaise trap in forest on the lower western slopes of Volcán Orosi in Guanacaste, and a male was reared close by from the larva of *Callionima denticulata* found feeding on *Tabernaemontana* 13584 (Apocynaceae) [97-SRNP-1375]. The last instar caterpillar was collected on 1 July 1997, and became a prepupa on 5 July 1997; it was consumed by the wasp larva a few days later. The wasp spun a cocoon in the prepupal cocoon in the litter, from which an adult emerged on 16 October 1997. A second unidentified *Thyreodon* parasitized a *C. denticulata* caterpillar at the site of the above-mentioned Malaise trap capture [88-SRNP-495]. However, either *C. denticulata* is not the sole host of *T. schauffi* or this wasp species is restricted to the western middle-elevation slope of Volcán Orosi and Volcán Cacao. We conclude this because more than 100 *C. denticulata* caterpillars of all instars reared from

the (yet wetter) middle-elevation rain forests on the eastern side of the same volcanoes have yielded only Tachinidae as parasites.

**Material examined:** Holotype ♀, COSTA RICA, Guanacaste Prov., Guanacaste National Park, Estacion Maritza, on W side Volcán Orosi, 560 m, vi.1989 (Gauld & Mitchell) (BMNH). Paratypes: COSTA RICA: Guanacaste Prov.: 1 ♂, Guanacaste National Park, reared as per data above (Janzen & Hallwachs) (JHVC); 1 ♂, Guanacaste National Park, Sector Cacao, Sendero Nayo, 1000 m, x.1997 (Moraga) (BMNH).

#### 16. *THYREODON RIVINAE* PORTER

*Thyreodon rivinae* Porter, 1980: 243. Holotype ♀, USA, TEXAS (FSCA) [examined].

*Athyreodon rivinae* (Porter) Porter, 1989: 298.

Fore wing length 16.5–18.2 mm; clypeus weakly convex, with margin flared outwards, with apex pointed medially; malar space about 0.1 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and flattened; lower face centrally finely punctate; frons swollen between antennal sockets, with a weak to moderately sharp median vertical ridge, and with a low carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rather smooth; ocelli very large, the lateral ocellus contiguous with eye; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end only weakly raised, not reaching hypostomal carina; antenna setaceous, with 51–53 flagellomeres, the 20th subquadrate, 0.9–1.0 times as long as broad, the subapical ones with setae which are slightly shorter than the diameter of the flagellomere. Pronotum short with anterior margin moderately strongly and broadly reflexed, and with posterior margin centrally swollen, slightly angular, separated from the anterior margin by a broad U-shaped groove (Fig. 24); epomia absent; propleuron very sparsely punctate, with lower corner rounded, peripherally not impressed; mesoscutum finely punctate, with sharply impressed, deep notauli which are close together posteriorly, inner anterior margin of notaulus unspecialized; scuto-scutellar groove very deep, laterally margined by a strongly raised, simple, thickened carina; scutellum finely punctate, weakly convex; mesopleuron finely punctate, without a sharp sternal impression; metapleuron finely punctate, sometimes with a few obscure diagonal ridges; propodeum laterally slightly flattened, reticulate with interstices coriaceous, with a low rounded ridge above and behind the spiracle; propodeum posterodorsally rugose-reticulate, with transverse rugae posterolaterally, centrally with a very shallow median longitudinal

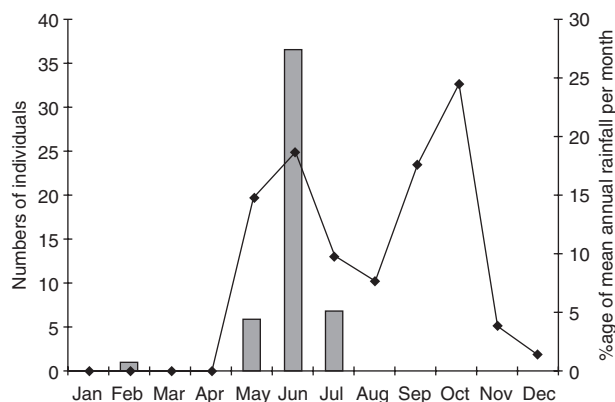
impression. Fore leg of female slender, with coxa without a rounded protuberance behind trochanteral insertion; 5th tarsomere 0.4–0.5 times as long as the preceding two tarsomeres, with tarsal claw quite short, with fine, close pectinae; hind coxa in profile moderately large, its hind end projecting slightly beyond level of hind end of propodeum; hind femur slender, about 6 times as long as maximally deep. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.1–1.2 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly subcylindrical; tergite II, in lateral view, 2.1–2.3 times as long as posteriorly deep. Male unknown.

A blackish brown species with flagellum bright yellow; wings basally and apically blackish infumate, centrally almost hyaline.

**Remarks:** Structurally *Thyreodon rivinae* closely resembles *T. maculipennis*. Both lack strong interantennal carinae, and an epomia, and both have the fore leg slender with the 5th tarsomere slightly shorter than the 3rd. Both also have the fore wing peripherally dark but centrally hyaline. *T. rivinae* differs most conspicuously from *T. maculipennis* in having the posterior ocelli contiguous with the eyes, and the flagellum yellow (orange in living specimens).

**Biological notes:** Although *Thyreodon rivinae* is common at the lights in ACG dry forest from late May to early July (and almost no others have been collected, suggesting strong univoltinism) (Fig. 65), none has been reared from thousands of sphingid caterpillars and many tens of species of sphingids reared from the ACG dry forest.

Either *T. rivinae* probably parasitizes one of the few species of Sphingidae whose caterpillar has not yet been encountered or it parasitizes one of the few spe-



**Figure 65.** The total numbers of individuals of *Thyreodon rivinae* collected at light by month between 1985 and 1992 in Sector Santa Rosa of the ACG compared with the monthly percentage of the annual rainfall.

cies not yet frequently sampled. The obvious candidate for the latter is *Erinnyis obscura*, only ten caterpillars of which have been reared. One of these was parasitized by a small *Thyreodon* that died in its cocoon [94-SRNP-3289]. *E. obscura* feeds on herbaceous asclepiadaceous vines in insolated early successional stages, a distinctive common microhabitat from which no sphingid-parasitizing species of *Thyreodon* has been reared.

*Material examined*: Holotype ♀, USA, TEXAS, Hidalgo County, Bentsen Rio Grande Valley State Park, vii.1979 (Porter) (FSCA).

Non-type material: COSTA RICA: Guanacaste Prov.: 2 ♀, 3 km E Cuajiniquil, 300 m, vi.1992 (*Parataxonomists*) (INBio); 2 ♀, Guanacaste National Park, Estacion Murcielago, 8 km SW Cuajiniquil, 100 m, vi.1992 (*Parataxonomists*) (INBio); 4 ♀, Guanacaste National Park, Finca Jenny, 30 km N Liberia, 240 m, vi.1991, vi–vii.1992, vii.1993 (*Espinoza & Araya*) (INBio); 2 ♀, Guanacaste National Park, Sector Santa Rosa, caught as adult but listed in data-base as 99-SRNP-8560, 99-SRNP-9078 (*Franco*) (JHVC); 2 ♀, Lomas Barbudal, 30 m, vii.1991 (*Chavarría*) (INBio); 2 ♀, Santa Rosa National Park, 300 m, vi.1980, vi.1984 (*Janzen & Hallwachs*) (BMNH); 23 ♀, same locality, v–vi.1985 (*Janzen & Hallwachs*) (INBio); 9 ♀, same locality, vi.1985, vii.1986, vi.1989 (*Gauld*) (BMNH); 10 ♀, Santa Rosa National Park, 300 m, ii.1992, vi–vii.1992 (*Parataxonomists*) (INBio).

#### 17. *THYREODON MACULIPENNIS* CRESSON

*Thyreodon maculipennis* Cresson, 1874: 375. Lectotype ♀, MEXICO, designated by Townes & Townes, 1966: 189 (PANS) [examined].

Fore wing length 15.2–19.1 mm; clypeus weakly convex, with margin flared outwards, with apex pointed medially; malar space about 0.3 times basal mandibular width; maxillary palp long with second palpomere strongly broadened and flattened; lower face centrally finely and sparsely punctate; frons swollen between antennal sockets, with a weak to moderately sharp median vertical ridge, and with a low carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rather smooth; ocelli large, the lateral ocellus separated from eye by about 0.3 times its own maximum diameter; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end weakly raised, not reaching hypostomal carina; antenna setaceous, with 48–52 flagellomeres, the 20th subquadrate, about 1.0 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin moderately

strongly and broadly reflexed, and with posterior margin centrally swollen, but not angulate, separated from the anterior margin by a broad U-shaped groove; epomia absent; propleuron very sparsely punctate, with lower corner rounded, peripherally not impressed; mesoscutum finely punctate, with sharply impressed, deep notauli which are close together posteriorly, inner anterior margin of notaulus unspecialized; scuto-scutellar groove very deep, laterally margined by a strongly raised, simple, thickened carina; scutellum finely punctate, weakly convex; mesopleuron finely punctate, without a sharp sternular impression; metapleuron finely punctate, sometimes with a few obscure diagonal ridges; propodeum laterally slightly flattened, reticulate with interstices coriaceous, with a low rounded ridge above and behind the spiracle; propodeum posterodorsally reticulate, with transverse rugae posterolaterally, centrally with a very shallow median longitudinal impression. Fore leg of female slender, with coxa without a rounded protuberance behind trochanteral insertion, with 5th tarsomere 0.4–0.5 times as long as the preceding two tarsomeres, with tarsal claw quite short, with fine, close pectinae; hind coxa in profile moderately large, its hind end projecting slightly beyond level of hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.1–1.2 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly subcylindrical; tergite II, in lateral view, 2.1–2.6 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with fine sparse hair; claspers quite long, the distal part slightly tuned up-wards, the dorsal apex obliquely truncate, the lower margin not angulate before apex, the upper margin with a broad shallow notch, the part proximal to this slightly expanded (Fig. 53); aedeagus in profile with apex expanded, distally slightly flattened, with a lateral vertical sharp keel.

A blackish brown species with flagellum dark brownish, rarely with mesoscutum dark reddish brown; wings basally and apically blackish infumate, centrally almost hyaline.

*Remarks*: Structurally *Thyreodon maculipennis* closely resembles *T. rivinae*. Both lack strong interantennal carinae, and an epomia, and both have the fore leg slender with the 5th tarsomere slightly shorter than the 3rd. Both also have the fore wing peripherally dark but centrally hyaline. *T. maculipennis* differs most conspicuously from *T. rivinae* in not having the posterior ocelli contiguous with the eyes, and having the flagellum blackish or dark brown.



*Biological notes:* *Thyreodon maculipennis* is unambiguously a specialist on the small green caterpillars of *Perigonia ilus* (Sphingidae) in ACG dry forest [81-SRNP-65; 84-SRNP-1049; 84-SRNP-1289; 85-SRNP-280; 85-SRNP-280.1; 89-SRNP-316; 89-SRNP-744; 91-SRNP-1715; 91-SRNP-1720; 91-SRNP-1725; 91-SRNP-2042; 92-SRNP-2488; 93-SRNP-1660; 93-SRNP-4042; 98-SRNP-8361; 98-SRNP-9316; 01-SRNP-14556] (Table 2). Of 392 rearings of wild-caught *P. ilus* caterpillars, 9.9% were parasitized by this wasp, and 41% of the cocoons produced adult wasps. No other species of *Thyreodon* attacks *Perigonia ilus* in the ACG. *P. ilus* primarily feeds on the low foliage of *Calycophyllum candidissimum* (Rubiaceae), but is rarely found on a sympatric tree, *Guettarda macrospermum* (Rubiaceae). *T. maculipennis* parasitized *P. ilus* on both food plants. *Perigonia lusca* (which is extremely similar to *P. ilus*) usually feeds on *G. macrospermum* and only very rarely on *C. candidissimum*. There remains the remote possibility that some of the few '*P. ilus*' larvae feeding on *G. macrospermum* and parasitized by *T. maculipennis* were misidentified as *P. lusca*, but this is not the most parsimonious deduction. *Perigonia ilus* (and *P. lusca*) breed throughout the range of wild-caught adults of *T. maculipennis* caught in other parts of Costa Rica.

*Material examined:* Lectotype ♀, MEXICO: Orizaba (PANS).

Non-type material: COSTA RICA: Guanacaste Prov.: 1 ♀, 1 ♂, Barra Honda National Park, 3 km NW Nacacome, 100 m, vii, x–xi.1992 (Reyes) (INBio); 1 ♀, Guanacaste National Park, Los Almendros, 300 m, vi.1994 (Lopez) (INBio); 8 ♀, 9 ♂, Guanacaste National Park, reared as per data above (Janzen & Hallwachs) (JHVC); 2 ♀, Guanacaste National Park, Finca Jenny, 31 km N Liberia, 240 m, vi–vii.1992, vi–vii.1995 (Araya) (INBio); 2 ♀, 2 ♂, Santa Rosa National Park, 300 m, v–vi.1985 (Janzen & Hallwachs) (INBio); 3 ♀, same locality, vi.1989 (Gauld) (BMNH); 1 ♀, same locality, vi.1992 (Parataxonomists) (INBio); 1 ♀, Refugio Palo Verde, 50 m, vii.1985 (Solis) (INBio): Puntarenas Prov.: 1 ♀, Carara Biological Reserve, Estacion Quebrada Bonita, 50 m, viii–ix.1989 (Gauld) (BMNH); 17 ♀, 11 ♂, same locality, v–vi.1990, v.1992, v.1993 (Zuñiga, Bello, Rojas & Saborio) (INBio); 1 ♂, Osa Peninsula, Corcovado National Park, Estacion Sirena, 0–100 m, vii.1992 (Saborio) (INBio).

#### 18. *THYREODON DARLINGI* GAULD SP. NOV.

[*Thyreodon* sp. 1 Gauld, 1988: 60.]

Fore wing length 17.9–22.1 mm; clypeus weakly convex, with apex flared outwards, bluntly pointed medially; malar space about 0.2 times basal mandibular width; maxillary palp long with second palpomere

strongly broadened and slightly inflated; lower face centrally finely punctate; frons weakly convex between antennal sockets, sometimes with a very weak median vertical carina, and without a carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally smooth; ocelli large, the lateral ocellus separated from eye by about 0.1–0.2 times its own maximum diameter; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, not reaching hypostomal carina; antenna setaceous, with 49–52 flagellomeres, the 20th subquadrate, 1.0 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally swollen, forming an angular, centrally impressed ridge which is separated from the anterior margin by a deep U-shaped groove (Fig. 23); epomia possibly represented on upper part of pronotum by one of several rugae; propleuron sparsely punctate, with lower corner rounded, peripherally not impressed; mesoscutum highly polished, finely and sparsely punctate, with notauli narrow and deeply impressed, posteriorly confluent, anteriorly without a lateral or transverse crest; scuto-scutellar groove very deep, laterally margined by a very strongly raised, simple carina, scutellum polished, finely punctate, weakly convex; mesopleuron highly polished, finely and sparsely punctate, with a trace of a sternaular impression anteriorly and posteriorly, and usually with a slightly rugose or more closely punctate area extending obliquely back from upper end of epicnemial carina; metapleuron punctate with weak rugae; propodeum laterally weakly convex, with a sharp (and often rather smooth) low ridge above and behind the spiracle, rugose with the rugae tending to be parallel lower down; propodeum posterodorsally rugose-reticulate, with strong transverse rugae posterolaterally, centrally with a single shallow longitudinal impression. Fore leg of female rather stout, with coxa more or less without a protuberance behind trochantal insertion, with 5th tarsomere about 0.4–0.5 of length of preceding two tarsomeres, with tarsal claw moderately long and with moderately coarse, close pectinae; hind coxa in profile moderately large, its hind end extending well beyond hind end of propodeum; hind femur stout, about 6.0 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.1–1.4 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I slender, anteriorly subcylindrical; tergite II, in lateral view, 2.3–2.5 times as long as posteriorly deep. Male with subgenital plate small and convex, covered with sparse coarse

hair; claspers long, the dorsal apex elongately rounded/truncate, slightly inclined upwards without an apical spine-like projection, the lower margin weakly convex (Fig. 61); aedeagus in profile with apex expanded but flattened on extreme apex, with a very sharp lateral keel.

A polished black species with a blue-black metallic sheen; wings uniformly blackish infumate.

*Remarks:* *Thyreodon darlingi* is named in honour of D. Christopher Darling in recognition of his enthusiastic identification of the thousands of perilampid hyperparasite wasps reared by the ACG caterpillar inventory. *T. darlingi* rather closely resembles *T. delvarei* in general appearance and coloration. Both are shining black species with uniformly black wings and a slightly metallic sheen to the mesosoma, both have rather large ocelli, and the males of both species have a long, slightly bent clasper that lacks an apical spine, and have the apex of the aedeagus somewhat flattened. *T. darlingi* differs from *T. delvarei* in having larger ocelli that are separated from the eye margin by about 0.2 or less of their own maximum diameter, whereas those of *T. delvarei* are separated by about 0.7 of their maximum diameter. The malar space of *T. darlingi* is far narrower than *T. delvarei*, and it has strongly impressed notauli and the mesopleuron less smooth.

*Biological notes:* *Thyreodon darlingi* occurs well within the area of the ACG caterpillar rearing programme, but it has not yet been encountered in many thousands of caterpillars and many tens of species of sphingids reared from these low- to mid-elevation rain forest sites.

*Material examined:* Holotype ♀, COSTA RICA, Guanacaste Prov., Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, iii–iv.1993 (*Ríos*) (INBio). Paratypes: COSTA RICA: Alajuela Prov.: 1 ♀, Colonia Libertad, Upala, iv.1988 (*Soto*) (UCRC); 1 ♀, Colonia Palmareña, 9 km SW Bajo Rodriguez, 700 m, vi.1996 (*Carballo*) (INBio); 3 ♀, 1 ♂, San Ramon, 800 m, ix.1994, iii.1997, vii.1998 (*Carballo*) (INBio); 3 ♀, Finca San Gabriel, 2 km W Dos Rios, 600 m, v.1989 (*Gauld & Mitchell*) (BMNH); 1 ♀, San Ramon de Dos Rios, 620 m, iv–v.1995 (*Cano*) (INBio); 2 ♀, 2 ♂, Estacion San Ramon Oeste, 620 m, iv.1994 (*Quesada*) (INBio); 2 ♀, Rio San Lorencito, San Ramon, 5 km N Colonia Palmareña, 900 m, iii.1990, vi.1993 (*Parataxonomists*) (INBio): Guanacaste Prov.: 1 ♀, 1 ♂, Guanacaste National Park, Estacion Pitilla, 680 m, iii–v.1989 (*Gauld & Mitchell*) (BMNH); 3 ♀, 1 ♂, Guanacaste National Park, Estacion Pitilla, 9 km S Sta Cecilia, 700 m, iii.1990, iii.1991, iv.1995 (*Ríos & Moraga*) (INBio).

#### 19. *THYREODON CARMEANI* GAULD SP. NOV.

*Thyreodon atriventris* (Cresson) 'dark morph' Gauld, 1988: 56.

Fore wing length 22.8–24.3 mm; clypeus rather flat, with apex out-flared, with a rounded point medially; malar space more or less obliterated; maxillary palp long, with second palpomere strongly broadened and slightly inflated; lower face centrally finely punctate; frons with a single weak vertical crest between antennal sockets and without a low carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli very large, the lateral ocellus contiguous with eye; head in dorsal view with gena rather abruptly rounded behind eye, occipital carina strong, its lower end sharp, but not reaching hypostomal carina; antenna setaceous, with 58–59 flagellomeres, the 20th slightly elongate, 1.1–1.2 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally weakly swollen, forming a low rounded ridge which is separated from the anterior margin by a deep U-shaped groove; epomia absent; propleuron sparsely punctate, with lower corner rounded, peripherally not impressed, slightly flared outwards; mesoscutum finely and sparsely punctate, with narrow, shallow, slightly transversely striate notauli which are almost confluent posteriorly, inner anterior margin of notaulus unspecialized; scuto-scutellar groove moderately deep, long, laterally margined by thickened, simple carinae; scutellum smooth, very finely punctate, rather flat and broad posteriorly; mesopleuron finely punctate, with a few weak foveae behind epicnemial carina, sternaulus sharply impressed anteriorly, narrow and posteriorly evanescent; epicnemial carina curving to meet anterior margin of pleuron above lower corner of pronotum; metapleuron dorsally rugose, finely punctate ventrally; propodeum laterally slightly flattened, very coarsely reticulate, with a sharp strongly raised tubercle above and behind the spiracle; propodeum posterodorsally very coarsely reticulate, with a median anterior tubercle, centrally without a trace of a shallow longitudinal impression. Fore leg of female rather slender, with coxa with a bluntly rounded, low protuberance behind trochanteral insertion, with 5th tarsomere 0.7–0.8 times as long as preceding two tarsomeres, with tarsal claw unusually short and with fine, moderately close pectinae; hind coxa in profile moderately large, its hind end projecting well behind level of hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.10–1.15 times as long as

abscissa of *Cu1* between *cu-a* and *1m-cu*. Metasoma with tergite I moderately slender, anteriorly subcylindrical or slightly dorsoventrally depressed; tergite II, in lateral view, 2.6–2.7 times as long as posteriorly deep. Male unknown.

An entirely black species with wings blackish brown infumate, more purplish basally, and with a central hyaline area.

*Remarks:* *Thyreodon carmeani* is named in honour of David Carmean, in recognition of his enthusiastic identification of the trigonalid hyperparasite wasps reared by the ACG caterpillar inventory. In an earlier work (Gauld, 1988) this species was treated as possibly being a dark morph of *T. atriventris*, which it closely resembles in general appearance and sculpture. However, now we have seen a second specimen we are certain it is distinct. It differs from *T. atriventris* in having the second discal cell in the fore wing shorter, and deeper, with *Cu1a* between *Cu1b* and *2m-cu* only 1.10–1.15 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*, whereas in *T. atriventris* this cell is slender and the abscissa of *Cu1a* between *Cu1b* and *2m-cu* is 1.65–1.95 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*. *T. carmeani* also has the tarsal claws shorter than other species in the genus, and it has tergite II much longer and more slender than that of *T. atriventris*.

*Biological notes:* *Thyreodon carmeani* has only been collected in Braulio Carrillo National Park, Costa Rica, between 700 and 1100 m, on two occasions in April and December. On both occasions it was taken at a mercury vapour light, suggesting it is at least crepuscular, and the enlarged ocelli and eyes suggest it may be active in the dark, even though it is black in colour. The host of this species is unknown.

*Material examined:* Holotype ♀, COSTA RICA, San José Prov., Braulio Carrillo National Park, Estacion Carrillo, 700 m, iv.1985 (*Chacón*) (INBio). Paratype: COSTA RICA: San José Prov.: 1 ♀, Braulio Carrillo National Park, La Montura, 1100 m, xii.1981 (*Janzen & Hallwachs*) (BMNH).

#### 20. *THYREODON RUFOTHORAX* CAMERON **STAT. NOV.**

*Thyreodon rufothorax* Cameron, 1886: plate 12. Holotype ♀, PANAMA (BMNH) [examined].

*Thyreodon rufithorax* Cameron: Cameron, 1886: 290. [Mis-spelling of *rufothorax*.]

*Tipulophion rufithorax* (Cameron) Schulz, 1903: 249. [Mis-spelling of *rufothorax*.]

[*Thyreodon atriventris* (Cresson) Townes & Townes, 1966: 186. Misidentification.]

Fore wing length 20.7–22.2 mm; clypeus rather flat, with apex out-flared, with a rounded point medially;

malar space more or less obliterated; maxillary palp long, with second palpomere strongly broadened and slightly inflated; lower face centrally finely punctate; frons with a single weak vertical crest between antennal sockets and without a low carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli very large, the lateral ocellus contiguous with eye; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, but not reaching hypostomal carina; antenna setaceous, with 53–54 flagellomeres, the 20th slightly elongate, 1.1–1.2 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally weakly swollen, forming a low rounded ridge which is separated from the anterior margin by a deep U-shaped groove; epomia absent; propleuron sparsely punctate, with lower corner rounded, peripherally not impressed but slightly flared outwards; mesoscutum finely and sparsely punctate, with narrow, shallow, slightly transversely striate notauli which are almost confluent posteriorly, inner anterior margin of notaulus unspecialized; scuto-scutellar groove moderately deep, long, laterally margined by thickened, simple carinae; scutellum smooth, very finely punctate, rather flat; mesopleuron finely punctate, usually with a rather shallow sternaular impression, sometimes this impression obsolescent; metapleuron finely punctate to granulate, with a few rugae dorsally; propodeum laterally slightly flattened, very coarsely reticulate, with a sharp strongly raised tubercle above and behind the spiracle; propodeum posterodorsally very coarsely reticulate, centrally without a trace of a shallow longitudinal impression. Fore leg of female rather slender, with coxa with a very low, bluntly rounded protuberance behind trochanteral insertion, with 5th tarsomere 0.5–0.6 times as long as preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind coxa in profile moderately large, its hind end projecting well behind level of hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu1a* between *Cu1b* and *2m-cu* 1.50–1.60 times as long as abscissa of *Cu1* between *cu-a* and *1m-cu*. Metasoma with tergite I moderately slender, anteriorly subcylindrical or slightly dorsoventrally depressed; tergite II, in lateral view, 1.5–1.7 times as long as posteriorly deep. Male with subgenital plate small and convex, with rather sparse hair; claspers quite long, the dorsal apex produced into a short spine-like projection, the lower margin rounded, not



angulate before apex; aedeagus in profile with apex expanded, apically weakly flattened, with a sharp lateral keel.

A mainly orange-brown species with interocellar area, flagellum, metasoma, and hind leg blackish brown, fore and mid tarsus slightly infuscate; wings hyaline with basal cell, distal 0.5 or so of marginal cell and proximal part of 3rd submarginal cell blackish infumate.

*Remarks:* *Thyreodon rufothorax* is easily separated from most other *Thyreodon* by the combination of its very large ocelli and eyes (which are contiguous, and the latter occlude the malar space almost entirely), coloration and pattern of the fore wings (Fig. 9). However, in these features and most others, it closely resembles *T. atriventris* and the two species are widely intermingled in museum collections of wild-caught '*T. atriventris*'; it was discussed under this species earlier (Gauld, 1988). Both sexes of the two species are most easily separated by the wing colour pattern, and the colour of the hind coxa, which is black in *T. rufothorax* and orange-brown in *T. atriventris*. Additionally, the male claspers of *T. rufothorax* do not have the pronounced ventral angulation found in all individuals of *T. atriventris* (Figs 62, 63).

*Biological notes:* *Thyreodon rufothorax* is a Mesoamerican species that occurs in both Panama and Costa Rica (and possibly further afield, but as it has frequently been confused with *T. atriventris*, other locality records require verification). In Costa Rica it occurs below about 600 m elevation (and is sympatric over this range with *T. atriventris*). This broad geographical range is congruent with the broad range of its known host caterpillars (see below). It comes frequently to lights placed out in the forest, which, coupled with its large size and gaudy colour, is the reason why there are so many individuals in the INBio collections (see below). From this we also deduce that it searches for caterpillars at night (as well as possibly in the daytime). It (and/or *T. atriventris*) has been encountered in the daytime visiting the fly- and wasp-pollinated flowers of *Allophylus occidentalis* (Sapindaceae), *Forsteronia spicata* (Apocynaceae) and *Trigonia rugosa* (Trigoniaceae) (along with *Rhynchophion flammipennis*).

All but one rearing record of *Thyreodon rufothorax* are from caterpillars of *Pachylioides resumens* (Sphingidae) [81-SRNP-664; 82-SRNP-598; 89-SRNP-393; 91-SRNP-2439; 99-SRNP-7108; 01-SRNP-14720] (Janzen & Hallwachs, 2003). These caterpillars were feeding on *Forsteronia spicata* (Apocynaceae), a common woody vine in the understorey (saplings) and upper levels of secondary successional dry forest in Sector Santa Rosa of the ACG. Of 229 wild-caught dry forest *Pachylioides resumens* caterpillars, 5% were

attacked by *T. rufothorax* (Table 2). However, 3% of these 229 caterpillars were killed by tachinid fly larvae before they reached the prepupal stage, and a few of these caterpillars may therefore have had *T. atriventris* larvae in them (nothing is known of the competitive abilities of young *Thyreodon* larvae in the face of co-occupation of a caterpillar by tachinid fly larvae). The single rearing from *Pachygonidia drucei* is from a total sample of ten larvae (*P. drucei* is a very low-density larva wherever it is found), and it was feeding on the rare woody vine *Doliodarpus dentatus* (Dilleniaceae) in the same dry forest with the *Pachylioides resumens* caterpillars. The large green caterpillars of *P. resumens* and *P. drucei* are superficially very similar in shape, weight and body size (see photographs in Janzen & Hallwachs, 2003). Both caterpillars make a shallow and nearly silk-free pupation chamber in the litter, and *T. rufothorax* spins its large, hard, tough cocoon in the centre of this chamber. The caterpillars that were parasitized ranged from second to last (fifth) instar when captured.

Not enough *Pachylioides resumens* and *Pachygonidia drucei* larvae have been reared from the ACG rain forest (five and five, respectively) to know if it even uses these two caterpillars there, much less at what frequency it might occur. Because more than 15 000 other sphingid larvae of about 65 species have been reared from the ACG dry forest, we feel comfortable in concluding that *P. resumens* and *P. drucei* are the sole species attacked by *T. rufothorax*. Both of these species of caterpillars occur throughout the Costa Rican range of *T. rufothorax* collected as adults at lights.

*T. rufothorax* stays in the cocoon for 41–89 days (in one case, 332 days) (Janzen & Hallwachs, 2003). Lineages that eclose within 1.5–3 months are probably having 2–3 generations during the rainy season, as both species of host caterpillars are among those that have 2–3 consecutive generations during the rainy season (rather than being univoltine or migrating out of the dry forest by the middle of the rainy season). The wasps that remain about 1 year in the cocoon are being univoltine. These generalizations are based on four *T. rufothorax* that eclosed after parasitizing *P. resumens*, one that eclosed after parasitizing *P. drucei* and four more that only survived to the cocoon stage after parasitizing *P. resumens* (the cocoons of *T. rufothorax* can be distinguished by being slightly smaller and less angular than are those of *T. atriventris*). We have no knowledge of adult survival, but adults are not encountered at light or in Malaise traps during the dry season (a season when there are no dry forest *P. resumens* or *P. drucei* caterpillars), and are most common at lights during the early rainy season, when they are presumably eclosing from cocoons spun either at the beginning or the end of the

previous rainy season. In short, *T. rufothorax* has 2–3 generations per 6-month rainy season but some individuals behave in an univoltine manner.

The biology of *T. rufothorax* is nearly identical to that of *T. atriventris*, except for the choice of caterpillars to parasitize. Two *Cidaphus rostratus* (Ichneumonidae: Mesochorinae) have been reared as hyperparasites of *T. rufothorax* [86-SRNP-176.1, 93-SRNP-2308]. The host caterpillars were collected as third instars feeding on *Forsteronia spicata*. The newly eclosed hyperparasites cut exit holes in the anterior end of the *T. rufothorax* cocoon 1 or 2 years after spinning. The cocoon was in a dry bottle at ambient temperature inside a non-airconditioned house in the forest. *C. rostratus* is the only species of hyperparasite entered in the inventory that remains more than 1 year in the cocoon (and see *Thyreodon sharkeyi*).

**Material examined:** Holotype ♀, PANAMA, Bugaba, 260–500 m (*Champion*) (BMNH).

Non-type material: COSTA RICA: Alajuela Prov.: 1 ♂, Caño Negro, 20 m, v.1993 (*Martinez*) (INBio); 1 ♀, Monteverde, Estacion Laguna Pocosol, 850 m, vii.1991 (*Bello*) (INBio); Guanacaste Prov.: 2 ♂, Barra Honda National Park, 3 km NW Nacaome, 100 m, vii.1992 (*Reyes*) (INBio); 1 ♀, Guanacaste National Park, Estacion Los Almendros, 300 m, v.1994 (*López*) (INBio); 3 ♀, 3 ♂, Guanacaste National Park, reared as per data above (*Janzen & Hallwachs*) (JHVC); 1 ♀, 2 ♂, Guanacaste National Park, Estacion Maritza, W slope Volcán Orosi, 560 m, vi, viii.1990 (*Blanco*) (INBio); 3 ♀, 6 ♂, Guanacaste National Park, Estacion Murcielago, 8 km SW Cuajiniquil, 100 m, vi.1994 (*Caño*) (INBio); 1 ♀, Guanacaste National Park, Estacion Pitilla, 680 m, iii–iv.1989 (*Gauld & Mitchell*) (BMNH); 5 ♀, Guanacaste National Park, Estacion Pitilla, 9 km S Santa Cecilia, 700 m, iv.1990, iii–iv.1992, v.1993, iv.1995 (*Rios & Moraga*) (INBio); 6 ♀, 1 ♂, Guanacaste National Park, Finca Jenny, 30 km N Liberia, 240 m, vii.1992, vii.1993 (*Araya*) (INBio); 8 ♀ 5 ♂, Santa Rosa National Park, 300 m, v–vi.1985 (*Janzen & Hallwachs*) (INBio); 4 ♀, 1 ♂, same locality, vi.1989 (*Gauld & Mitchell*) (BMNH); 3 ♀, 2 ♂, same locality, vi–vii.1990, vi.1992 (*Parataxonomists*) (INBio); 3 ♀, 3 ♂, same locality, reared as per data listed above (*Janzen & Hallwachs*) (JHVC); Heredia Prov.: 1 ♀, La Virgen del Socorro, 1.5 km SE Cariblanco, 0 m, ii.1997 (*Janzen*) (INBio); Limón Prov.: 1 ♀, 4 ♂, Cerro Cocori, Finca Rojas, 150 m, iv–v.1992, vii.1993, iii.1994 (*Rojas*) (INBio); Puntarenas Prov.: 1 ♂, Estacion Aguas, Sendero Perruja, 300 m, iii.1998 (*Azofeifa*) (INBio); 1 ♂, Finca Cafrosa, 1.7 km E Escuela de Progreso, 1270 m, iii.1996 (*Chinchilla*) (INBio); 2 ♂, Finca Cafrosa, Embalce, 800 m NW de Tigra, 1280 m, iii.1996 (*Navarro*) (INBio); 4 ♀, 1 ♂, Carara Biological Reserve, Estacion Quebrada Bonita, 50 m, viii–x.1989

(*Gauld*) (BMNH); 18 ♀, 5 ♂, same locality, v–vi.1990, v, xi.1992 i.1994 (*Parataxonomists*) (INBio); 1 ♂, Osa Peninsula, Bosque Esquinas, 200 m, iii.1994 (*Segura*) (INBio); 1 ♀, Osa Peninsula, Corcovado National Park, Estacion Sirena, 0–100 m, x.1989 (*Gauld*) (BMNH); 7 ♀, 1 ♂, same locality, i.1990, viii.1991, i, v, xi.1993, iv.1994, iv.1995 (*Parataxonomists*) (INBio); 1 ♀, Osa Peninsula, Estacion Esquinas, 0 m, ii.1993 (*Segura*) (INBio); 8 ♀, 13 ♂, Osa Peninsula, Rancho Quemado, 200 m, i, viii, xii.1991, ii–iii, v.1992, xi.1993, v.1994 (*Marin & Quesada*) (INBio).

## 21. *THYREODON ATRIVENTRIS* (CRESSON)

*Ophion atriventris* Cresson, 1874: 374. Holotype ♀, MEXICO (PANS) [examined].

*Athyreodon thoracicus* Ashmead, 1900a: 87. Holotype ♀, ECUADOR (USNM) [examined].

*Thyreodon grenadensis* Ashmead, 1900b: 270. Holotype ♀, GRENADA (BMNH) [examined].

*Macrophion ornatus* Szépligeti, 1905: 33. Lectotype ♂, BELIZE, designated by Townes & Townes, 1966: 186 (TM) [examined].

*Athyreodon atriventris* (Cresson) Hooker, 1912: 102.

[*Macrophion fulvescens* (Cresson) Morley, 1912: 14. Misidentification.]

*Macrophion grenadensis* (Ashmead) Morley, 1912: 15.

*Thyreodon atriventris* (Cresson) Townes & Townes, 1966: 186.

Fore wing length 21.8–27.8 mm; clypeus rather flat, with apex out-flared, with a rounded point medially; malar space more or less obliterated; maxillary palp long, with second palpomere strongly broadened and slightly inflated; lower face centrally finely punctate; frons with a single weak vertical crest between antennal sockets and without a low carina extending from outer rim of antennal sockets upwards, close to and parallel with eye margin; frons centrally rugose; ocelli very large, the lateral ocellus contiguous with eye; head in dorsal view with gena rather evenly rounded behind eye, occipital carina strong, its lower end sharp, but not reaching hypostomal carina; antenna setaceous, with 57–63 flagellomeres, the 20th slightly elongate, 1.1–1.2 times as long as broad, the subapical ones with setae which are longer than the diameter of the flagellomere. Pronotum short with anterior margin strongly and broadly reflexed, and with posterior margin centrally weakly swollen, forming a low rounded ridge which is separated from the anterior margin by a deep U-shaped groove; epomia absent; propleuron sparsely punctate, with lower corner rounded, peripherally not impressed, slightly flared outwards; mesoscutum finely and sparsely punctate, with narrow, shallow, slightly transversely striate notauli which are almost confluent posteriorly, inner

anterior margin of notaulus unspecialized; scuto-scutellar groove moderately deep, long, laterally margined by thickened, simple carinae; scutellum smooth, very finely punctate, rather flat and broad posteriorly; mesopleuron finely punctate, with a rather broad, shallow, and slightly transversely striate sternaular impression; metapleuron finely punctate to granulate, with a few rugae dorsally; propodeum laterally slightly flattened, very coarsely reticulate, with a sharp strongly raised tubercle above and behind the spiracle; propodeum posterodorsally very coarsely reticulate, with a median anterior tubercle, centrally without a trace of a shallow longitudinal impression. Fore leg of female rather slender, with coxa with a bluntly rounded, low protuberance behind trochantal insertion, with 5th tarsomere 0.7–0.8 times as long as preceding two tarsomeres, with tarsal claw long and with fine, close pectinae; hind coxa in profile moderately large, its hind end projecting well behind level of hind end of propodeum; hind femur slender, about 6 times as long as maximally deep; hind tarsus of male with dense, moderately long pubescence ventrally. Fore wing with abscissa of *Cu*1a between *Cu*1b and *2m-cu* 1.65–1.95 times as long as abscissa of *Cu*1 between *cu-a* and *1m-cu*. Metasoma with tergite I moderately slender, anteriorly subcylindrical or slightly dorsoventrally depressed; tergite II, in lateral view, 1.5–1.7 times as long as posteriorly deep. Male with subgenital plate small and convex, with rather sparse hair; claspers quite long, the dorsal apex produced into a moderately long spine-like projection, the lower margin quite sharply angulate before apex; aedeagus in profile with apex expanded, apically weakly flattened, with a sharp lateral keel.

A mainly orange-brown species with interocellar area, flagellum, metasoma, hind femur, tibia and tarsus blackish brown, fore and mid tarsus slightly infuscate; wings hyaline with basal cell, distal 0.7 or so of marginal cell and proximal part of 3rd submarginal cell blackish infumate.

*Variation:* Two wild-caught individuals from ACG dry forest are smaller than normal (fore wing length about 17 mm) with fewer flagellomeres (49–51), a slightly less reticulate propodeum and more reddish hind femora. The status of these specimens is not clear, but they may represent another cryptic species. They are listed separately below.

*Remarks:* *Thyreodon atriventris* is very similar to *Thyreodon rufothorax*, and these taxa are easily distinguished from other species by the combination of very large ocelli and eyes (which are contiguous, and the latter occlude the malar space almost entirely), coloration and pattern of the fore wings. These two species have been consistently grouped together under the name *T. atriventris* in museum collections, a syn-

onymy formally proposed by Townes (Townes & Townes, 1966) and repeated in Gauld (1988). Here we demonstrate that the two are distinct species. *T. atriventris* and *T. rufothorax* are most easily distinguished by the colour of the hind coxa, which is orange-brown in *T. atriventris* and black in *T. rufothorax*. Additionally, the claspers of the male genitalia of *T. atriventris* have a pronounced and externally visible ventral angulation that is lacking in *T. rufothorax* (Figs 62, 63). *T. atriventris* also usually has the basal cell of the fore wing more or less entirely darkly infumate (Fig. 10), whereas *T. rufothorax* has this cell partially hyaline or only weakly palely infumate (Fig. 9). Finally, they are parasitoids of different species of caterpillars (see below).

*Biological notes:* *Thyreodon atriventris* is a wide-ranging species that definitely occurs from Mexico south to Ecuador, as do its two species of Moraceae-eating host caterpillars. It occurs throughout Costa Rica below about 600 m elevation (and is sympatric over this range with its sibling, *Thyreodon rufothorax*). It comes frequently to lights placed out in the forest, which, coupled with its large size and gaudy colour, is the reason why there are so many individuals in the INBio collections (see below). From this we also deduce that it searches for caterpillars at night (as well as possibly in the daytime). It (and/or *T. rufothorax*) has been encountered in the daytime visiting the fly- and wasp-pollinated flowers of *Allophylus occidentalis* (Sapindaceae), *Forsteronia spicata* (Apocynaceae) and *Trigonia rugosa* (Trigoniaceae) (along with *Rhynchophion flammipennis*).

All 35 rearing records of *Thyreodon atriventris* are from caterpillars of *Pachylia ficus* and *Pachylia syces* (Sphingidae) [e.g. 78-SRNP-81; 81-SRNP-316a; 85-SRNP-417; 86-SRNP-192; 86-SRNP-214; 91-SRNP-1341; 93-SRNP-2508; 93-SRNP-2645; 94-SRNP-3699; 94-SRNP-4824; 99-SRNP-8461; 99-SRNP-8576; 99-SRNP-8699; 99-SRNP-8713; 99-SRNP-8715; 01-SRNP-14695; 01-SRNP-14701; 01-SRNP-14835; 01-SRNP-14836] (Janzen & Hallwachs, 2003). These caterpillars were feeding on *Brosimum alicastrum*, *Maclura tinctoria*, *Castilla elastica* and four species of *Ficus* (all in the Moraceae). These are all the Moraceae in ACG dry forest except for three more species of *Ficus*. These two large green caterpillars are superficially very similar, and it is possible that a few of the '*P. ficus*' records were in fact *P. syces* (the prepupa of *P. ficus* is brick red-orange dorsally, whereas the prepupa of *P. syces* is black and cream ringed with a red head). *Pachylia ficus* also has a 'rotten twig'-coloured morph as well as the (more common) green morph (see images in Janzen & Hallwachs, 2003), and *T. atriventris* has been reared from both colour morphs.



*Pachylia* caterpillars make a shallow and nearly silk-free pupation chamber in the litter, and *T. atriventris* spins its large hard, tough, cocoon in the centre of this chamber. Although all caterpillars that have been parasitized were penultimate or ultimate instar when collected, it is possible that parasitization occurs at an earlier instar because it does so with other species of *Thyreodon*. When univoltine, and therefore dormant through the 6-month dry season, the larva remains as a wasp prepupa in the cocoon until about 1 month before it ecloses.

*Thyreodon atriventris* has been reared from both ACG dry forest and rain forest. Although *Pachylia* caterpillars occur throughout the ACG, not enough have been found in the wetter areas to comment on the proportion of parasitization by *T. atriventris*. Of 387 wild-caught dry forest *Pachylia* caterpillars, 9% were attacked by *T. atriventris*. However, 13% of these 387 caterpillars were killed by *Cryptophion* wasps (Ichneumonidae) or by tachinid fly larvae before they reached the prepupal stage, and some of these caterpillars may also have had *T. atriventris* larvae in them.

*T. atriventris* stays in the cocoon for 30–41 days, 120–198 days or 292–350 days (Janzen & Hallwachs, 2003). Lineages that eclose in 1–1.5 months are probably having at least two generations in the first half of the rainy season (and could conceivably have another at the end of the rainy season). Those that eclose after 3–5 months may have a second generation during the end of the rainy season (a time when there are *Pachylia* larvae present, albeit at much reduced numbers as compared with the first 3 months of the rainy season). Those that remain about 1 year in the cocoon are being univoltine. We have no knowledge of adult survival, but adults are not encountered at light or in Malaise traps during the dry season (a time when there are no dry forest *Pachylia* caterpillars, even though *Ficus* at least stays evergreen), and are most common at lights during the early rainy season, when they are presumably eclosing from cocoons spun either at the beginning or at the end of the previous rainy season. In short, *T. atriventris* has 2–3 generations per 6-month rainy season but some individuals behave in a univoltine manner.

**Material examined:** Holotype ♀, (*Ophion atriventris* Cresson) MEXICO, Orizaba (PANS). Holotype ♀, (*Athyreodon thoracicus* Ashmead) ECUADOR (USNM). Holotype ♀, (*Thyreodon grenadensis* Ashmead). GRENADA, Baltasar, windward side (BMNH). Lectotype ♂ (*Macrophion ornatus* Szépliget) BELIZE 'British Honduras' (TM).

Non-type material: COSTA RICA: Alajuela Prov.: 2 ♀, 1 ♂, Finca San Gabriel, 2 km W Dos Rios, 600 m, vi.1988 (*Gauld & Mitchell*) (BMNH); 2 ♂, same

locality, vi.1989 (*Parataxonomists*) (INBio); 1 ♀, San Cristobal, 600–620 m, iii.1998 (*Quesada*) (INBio): Guanacaste Prov.: 1 ♂, Barra Honda National Park, 100 m, v.1988 (*Gauld*) (BMNH); 1 ♂, Barra Honda National Park, Los Mesones, 100 m, v.1995 (*Reyes*) (INBio); 4 ♂, Barra Honda National Park, 3 km NW Nacaome, 100 m, v.1993, viii.1994 (*Reyes*) (INBio); 5 ♀, 14 ♂, Guanacaste National Park, reared as per data above (*Janzen & Hallwachs*) (JHVC); 2 ♀, Guanacaste National Park, Estacion Los Almendros, 300 m, x.1993 (*López*) (INBio); 1 ♂, Guanacaste National Park, Cerro el Hacha, 400 m, xi–xii.1991 (*Lopez*) (INBio); 4 ♀, 5 ♂, Guanacaste National Park, Estacion Maritza, W slope Volcán Orosi, 560 m, vi, viii.1990, ii–iii.1992 (*Blanco*) (INBio); 2 ♀, 1 ♂, Guanacaste National Park, Estacion Murcielago, 8 km SW Cuajiniquil, 100 m, vi.1994 (*Caño*) (INBio); 6 ♀, 2 ♂, Guanacaste National Park, Estacion Pitilla, 9 km S Santa Cecilia, 700 m, x.1990, iv.1991, vi.1992, iv–v.1993 (*Rios & Moraga*) (INBio); 11 ♀, Guanacaste National Park, Finca Jenny, 30 km N Liberia, 240 m, vi–viii.1993, vi–vii.1995 (*Araya*) (INBio); 1 ♀, 1 ♂, Palo Verde, 10 m, vi–vii.1991 (*Chavarria*) (INBio); 1 ♀, same locality, vi.1988 (*Arguedas*) (UCRC); 3 ♀, 1 ♂, Rincon de la Vieja National Park, Estacion Las Pailas, 800 m, i.1993, v.1994 (*Taylor*) (INBio); 16 ♀, 6 ♂, Santa Rosa National Park, 300 m, v–vi.1985 (*Janzen & Hallwachs*) (INBio); 2 ♀, Tenorio Zona Protectora, Rio San Lorenzo, Tierras Morenas, 1050 m, i.1993, viii.1994 (*Rodriguez*) (INBio): Heredia Prov.: 1 ♀, Braulio Carrillo National Park, Estacion Magassay, 200 m, v.1991 (*Zumbado*) (INBio); 2 ♀, La Selva Biological Station, 50–150 m, iii–iv.1987 (*Chavarria*) (INBio); 1 ♀, same locality, iv.1989 (*Hespenheide*) (BMNH); 1 ♀, same locality, i.1992 (*Lezama*) (UCRC); 1 ♂, Los Arbolitos, 30 m, iii.1993 (*Araya*) (INBio): Limón Prov.: 1 ♀, 5 ♂, Tortuguero National Park, Cerro Tortuguero, 150 m, v.1990, x.1991, iv–v.1992, vii.1993, iii.1994 (*Delgado & Solano*) (INBio); 1 ♂, Amubri, 70 m, i.1994 (*Gallardo*) (INBio): Puntarenas Prov. 7 ♀, 5 ♂, Carara Biological Reserve, Estacion Quebrada Bonita, 50 m, viii–xi.1989 (*Gauld*) (BMNH); 22 ♀, 12 ♂, same locality, xii.1989, v–vi.1990, v–vi, xi.1992, viii.1993, i.1994 (*Parataxonomists*) (INBio); 1 ♀, 3 ♂, Cerro de Oro, Albergue, 50–150–170 m, v–viii.1995 (*Gamboia*) (INBio); 2 ♀, Estacion Agujas, Sendero Purraja, 300 m, xi.1997, iii.1998 (*Azofeifa*) (INBio); 6 ♀, 5 ♂, Osa Peninsula, Corcovado National Park, Estacion Sirena, 0–100 m, ix–xi.1989 (*Gauld*) (BMNH); 39 ♀, 5 ♂, same locality, x.1989, i.1990, xi.1991, i–v.1993, i.1994, viii.1995 (*Fonseca & Picado*) (INBio); 1 ♀, Osa Peninsula, Estacion Esquinas, 0 m, ii.1993 (*Segura*) (INBio); 2 ♀, 5 ♂, Osa Peninsula, Rancho Quemado, 200 m, viii, xii.1991 (*Marin & Quesada*) (INBio); 1 ♀, Quepos, Manuel Antonio National Park, ii.1993 (*Varela*) (INBio): San José Prov.: 1 ♀, Braulio Carrillo National Park, Estacion Carrillo, 730 m,

iii.1990 (*Chacón*) (INBio); 1 ♂, Braulio Carrillo National Park, Estacion Carrillo, 700 m, vii.1990 (*Parataxonomists*) (INBio); 1 ♂, 2.5 km W Ciudad Colon, 700–900 m, xii.1995 (*Rifkind*) (UCRC); 1 ♂, Pozo Azul, Rio Parrita, xii.1961 (*Wille*) (UCRC).

Small individuals: COSTA RICA: Guanacaste Prov.: 1 ♀, Guanacaste National Park, Finca Jenny, 31 km N Liberia, 240 m, vi.1993 (*Araya*) (INBio); 1 ♀, Santa Rosa National Park, 300 m, v.1985 (*Janzen & Hallwachs*) (INBio).

### THE CLADISTICS OF THE *THYREODON* GENUS-GROUP

The *Thyreodon* genus-group s.s. is putatively a monophyletic group comprising four genera, *Euryophion*, *Dictyonotus*, *Rhynchophion* and *Thyreodon* (Gauld, 1985). Although the first of these genera was always found to be the sister-lineage to the other three, the relationships of these last three genera was ambiguous with some support for both *Dictyonotus* + (*Rhynchophion* + *Thyreodon*) and *Rhynchophion* + (*Dictyonotus* + *Thyreodon*), although the more plausible characters favoured the latter hierarchy. In this section we re-examine the phylogenetic relationships of the four genera, and the Mesoamerican species of *Rhynchophion* and *Thyreodon* detailed above. We discuss this phylogeny in relation to host utilization. No details of the biology of the South American species are known. In general, most are very poorly collected, and often only known from damaged holotypes. Few species are clearly diagnosed (but see Porter, 1984), so we have made no attempt to include all described *Thyreodon* species in this study, although we have included a few exemplars of the more extensively collected species.

### TAXA AND CHARACTERS

For the purpose of this study a relatively plesiomorphic ophionine, *Ophion luteus* (L.) and the more derived ophionine *Enicospilus heliothidis* Viereck were used as out-groups. The primarily Afrotropical genus *Euryophion* was represented by three species, about which host information is available, *E. adustus* (Townes), *E. ikuthana* (Kriechbaumer) and *E. latipennis* (Kirby). The Old World genus *Dictyonotus* is represented by two species of known biology, *D. nigrocyaneus* (Tosquinet) and *D. purpurascens* (Smith), and the endemic New World genus *Rhynchophion* is represented by the two Mesoamerican species *R. flammipennis* (Ashmead) and *R. woodi* sp. nov. All 21 currently recognized Costa Rican species of *Thyreodon* have been included, as has the widespread North American species *T. atricolor* (Olivier), and the South American species: *T. boliviae* Morley, from

Bolivia and Peru; *T. cyaneus* (Brullé), widespread in South America; *T. nigrocaeruleus* Cameron from northern South America; and *T. ruficornis* (Brullé) from Brazil and northern Argentina. A total of 73 characters were used in the cladistic analysis. These are listed in Appendix 1, in which the presumed plesiomorphic condition is denoted by a '0', derived states by integers. The data matrix for character state distributions is given in Table 3.

### ANALYTICAL TECHNIQUE

Data were manipulated using WincladaVer. 0.9.99 (Nixon, 2000). The data were analysed searching for minimum-length trees under equal character weights using the NONA programme (version 1.6) of Goloboff (1999). NONA was run with all multistate characters, except nos. 11, 17, 18 and 69 (all of which are obviously transformation series), treated as non-additive. The heuristic search command **mult\*** (random addition sequence with tree bisection and reconnection) was implemented with 70 replications, with 12 trees held during each replication (**hold/**).

### RESULTS OF ANALYSIS

The analysis yielded 12 very similar cladograms with a length of 241 steps, a consistency index of 0.46 and a retention index of 0.76. The trees differed only in whether or not most *Thyreodon* species (excluding *T. woodleyi* and *T. papei*) formed a polytomy or a series of poorly resolved steps. The strict consensus (Nelson) tree is shown in Figure 66. This analysis confirmed the earlier results obtained by Gauld (1985) using fewer characters and different analytical methods. First, the *Thyreodon* genus-group is strongly monophyletic, supported by ten autapomorphies (nos. 1.1, 26.1, 33.1, 36.1, 39.1, 51.1, 56.1, 57.1, 58.1, 62.1). Second, *Euryophion* is the most basal lineage, and the sister-group to a monophyletic clade comprising the other three genera, which is supported by nine synapomorphies (nos. 3.1, 7.1, 11.2, 13.1, 20.1, 41.6, 53.2, 54.1, 63.1). Third, within this group, *Rhynchophion* is the sister-lineage to *Dictyonotus* + *Thyreodon*, with the terminal clade supported by three characters (nos. 9.1, 35.1, 66.1). Fourth, all genera are demonstrably monophyletic: *Euryophion* (autapomorphies – nos. 55.1, 61.1); *Rhynchophion* (nos. 4.1, 32.1, 67.1, 68.1, 72.2, 73.1); *Dictyonotus* (nos. 24.1, 30.1, 31.1, 34.1, 41.1, 45.1); *Thyreodon* (nos. 2.1, 5.1, 10.1, 17.2, 21.1, 22.2, 37.1, 42.1, 48.1, 57.0, 59.1).

Within *Thyreodon* the hierarchical resolution was fairly poor and somewhat ambiguous, but certain quite robust patterns were apparent. First, *Thyreodon woodleyi* and *Thyreodon papei* consistently emerged as the basal two species in the genus. Nine species (*T. darlingi*, *T. boliviensis*, *T. rivinae*,

**Table 3.** Data matrix for 36 species of Ophiominae used in cladistic analysis. Unknown conditions, usually because one sex was not available, are indicated by a '?', and variable conditions (coded as 0/1) by a '\*'

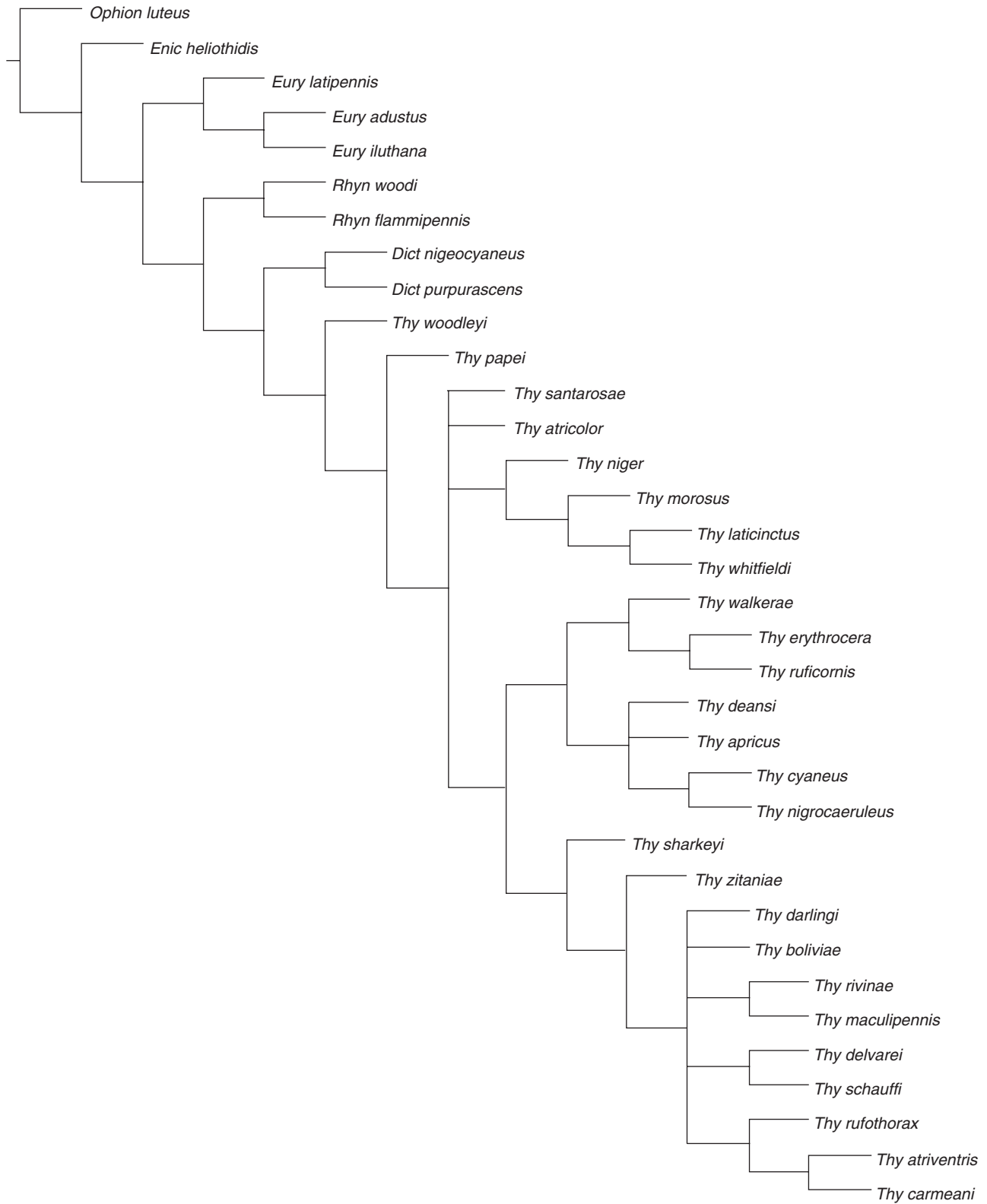
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39					
<i>Ophion luteus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Enicospilus heliothidis</i>	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Euryophion adustus</i>	1	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	2	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1			
<i>Euryophion ikuthana</i>	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1				
<i>Euryophion latipennis</i>	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	2	0	0	0	0	0	0	1	0	0	1	0	1				
<i>Dictyonotus nigrocyanus</i>	1	0	1	0	0	1	1	0	1	0	2	0	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	0	1	1	1	1	1	0	0	1			
<i>Dictyonotus purpurascens</i>	1	0	1	0	0	1	1	0	1	0	2	0	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	0	1	1	1	1	1	0	0	1			
<i>Rhynchophion flammipennis</i>	1	0	1	1	0	1	1	0	0	0	2	0	1	0	*	0	0	0	0	1	0	0	0	2	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1			
<i>Rhynchophion woodi</i>	1	0	1	1	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	2	1	0	0	2	1	0	0	0	0	0	1	1	0	0	1	0	0	1		
<i>Thyreodon atricolor</i>	1	1	1	0	1	1	1	0	1	1	2	0	1	1	2	1	0	1	1	1	2	0	0	1	2	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	1		
<i>Thyreodon atriventris</i>	1	1	1	0	1	1	1	0	0	0	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1		
<i>Thyreodon boliviana</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	0	1	2	0	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Thyreodon carneani</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	
<i>Thyreodon cyaneus</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Thyreodon darlingi</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Thyreodon dearsi</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Thyreodon delvareii</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
<i>Thyreodon erythroera</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Thyreodon laticinctus</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Thyreodon maculipennis</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Thyreodon morosus</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon niger</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon nigrocaeruleus</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon pappei</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon rufofornis</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon rufothorax</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon santarosae</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon schauffi</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon sharkyei</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon walkerae</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon whitfieldi</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon woodleyi</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Thyreodon zitaniae</i>	1	1	0	1	1	1	1	0	0	1	3	0	0	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Downloaded from https://academic.oup.com/zoolinmean/article/14/1/3/297/2624226 by guest on 31 August 2021



Table 3. Continued

	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73							
<i>Ophion luteus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0						
<i>Enicospilus heliothidis</i>	1	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Euryopinion adustus</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0				
<i>Euryopinion latipennis</i>	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0				
<i>Dictyonotus nigrocyanus</i>	1	1	0	0	0	1	1	0	0	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0			
<i>Dictyonotus purpurascens</i>	1	1	0	0	0	1	1	0	1	0	1	0	1	0	2	1	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0			
<i>Rhynchophion flammipennis</i>	1	6	0	0	0	1	1	0	1	0	0	1	1	2	1	0	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0		
<i>Rhynchophion woodi</i>	1	6	0	0	0	1	1	0	0	0	0	1	1	2	1	0	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0		
<i>Thyreodon apricus</i>	1	5	2	1	0	1	1	0	1	1	1	1	2	1	1	0	1	0	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0		
<i>Thyreodon atricolor</i>	1	2	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0		
<i>Thyreodon atriventris</i>	1	2	0	0	2	0	1	0	0	0	0	1	0	3	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0	2	1	1	0	0	0	0	0	0	0		
<i>Thyreodon boliviana</i>	1	5	1	0	2	0	1	0	0	1	0	1	3	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Thyreodon carneani</i>	1	2	0	0	2	0	1	0	0	1	0	0	1	3	1	0	1	0	1	0	0	0	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thyreodon cyaneus</i>	1	5	1	0	0	2	1	0	1	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thyreodon darlingtoni</i>	1	2	0	0	1	2	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	0	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thyreodon deansii</i>	1	5	1	1	0	1	1	0	1	1	0	1	2	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thyreodon delvareii</i>	1	4	1	0	1	2	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	0	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thyreodon erythroera</i>	1	5	0	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Thyreodon laticinctus</i>	1	4	1	0	0	1	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	1	1	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon maculipennis</i>	1	2	1	0	1	1	1	0	1	0	0	1	1	2	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon morosus</i>	1	4	1	0	1	1	0	1	1	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon niger</i>	1	5	1	0	0	1	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon nigrocaeruleus</i>	1	5	1	0	0	1	1	0	1	1	0	1	2	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon pappei</i>	1	2	1	0	0	1	1	0	1	1	0	1	2	1	2	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon ruinae</i>	1	5	1	0	0	2	1	0	1	1	0	1	2	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon ruficornis</i>	1	2	0	0	2	0	1	0	1	1	0	1	0	3	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon rufothorax</i>	1	3	0	0	0	1	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon santarosae</i>	1	4	1	0	1	2	1	0	0	1	1	1	1	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon schauffi</i>	1	5	1	0	0	1	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon sharkeyi</i>	1	5	1	0	0	1	1	0	1	1	0	1	2	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon walkeae</i>	1	9	1	0	0	1	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon whitfieldi</i>	1	9	1	0	0	1	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	1	3	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon woodleyi</i>	1	9	1	0	0	1	1	0	1	1	0	1	1	2	1	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyreodon zittaniae</i>	1	5	1	0	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	0	0	0	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0



**Figure 66.** The strict consensus (Nelson) tree.



**Figure 67.** Cocoon of *T. whitfieldi* (label shown is approximately 22 mm wide).

*T. maculipennis*, *T. delvarei*, *T. schauffi*, *T. rufothorax*, *T. atriventris* and *T. carmeani*) form a distinct monophyletic group. These have been treated (Porter, 1989) as comprising a separate genus, *Athyreodon*, but it is clear that to accord this species-group such status would render the restricted *Thyreodon* paraphyletic. We suggest it is best treated as the *atriventris* species-group. The *T. laticinctus* species-group *sensu* Porter (1984) was not recovered as monophyletic, but was found to be paraphyletic with respect to the *T. atriventris* species-group. *T. sharkeyi* was found to be the most basal member of a clade comprising it plus (*T. zitaniae* + *T. atriventris* species-group), whereas *T. apricus* clusters within a weakly supported complex of seven species, and *T. latipennis* and *T. morosus* belong to a third separate cluster of species. *T. santarosae* and the North American species *T. atricolor* were not associated with other species, but there is some support (nos. 15.1, 17.1) that they form a separate monophyletic group uniting with other taxa (except *Thyreodon woodleyi* and *Thyreodon papei*) as a basal polytomy.

### ZOOGEOGRAPHY

*Euryophion* is confined to the Afrotropical region except for one rather derived species that occurs in southern India (Gauld & Mitchell, 1981), whereas *Dictyonotus* occurs throughout the Afrotropical, Oriental and eastern Palaearctic (Gauld & Mitchell, 1977, 1981). Our analysis, coupled with the southern Palaearctic distribution of *Barytatocephalus*, the putative sister-genus of the *Thyreodon* genus-group, strongly

suggests an Old World origin for the group. Almost certainly the group radiated in the Tertiary, long after the break-up of Pangaea. The present distribution does not seem to reflect vicariance events, but is most easily explained by dispersal, eastwards into Asia and then into the New World probably via the Bering land bridge. Some evidence supporting our hypothesis is this fact that one species of *Dictyonotus* occurs as far north in Asia as 50°. Interestingly, some other Ophioninae, such as *Stauropogon*, have similar distributions (Gauld, 1988). Townes (1963), when discussing evidence for a Bering migration route for ichneumonids, points out that 64% of the species of Pimplinae (Ichneumonidae) present in Alaska also occur in the Palaearctic region.

### NATURAL HISTORY

Almost all species of Ophioninae are solitary larval koinobiont endoparasitoids of medium–small to very large caterpillars that feed externally on leaves. In all cases they wait until the caterpillar has passed into the prepupal state of the last instar and constructed a pupal chamber before beginning lethal (and fast) feeding. The final instar wasp larva then usually exits the empty host cuticle and spins its cocoon in the same pupation chamber that its host constructed, although a few species of *Enicospilus*, such as *E. glabratus* (Say), spin their cocoon within the host last instar larval cuticle (Gauld, 1988). The cocoons of most ophionines, including species of *Euryophion*, are ovoid, dark brown with a paler circumferential band, and are circular in cross-section. Those of *Thyreodon* and *Rhynchophion* are very hard dark ovoids with a very conspicuous hollow-chambered bulge on each side around the middle (Fig. 67). This form of cocoon is apparently a derived feature of this lineage. The hosts of the more basal ophionine genera, including most species of *Ophion* and *Enicospilus*, are principally the Noctuidae, although various other noctuid families are also parasitized, including the Arctiidae, Lymantriidae and Notodontidae. A few relatively derived lineages in the *Enicospilus* genus-group (*sensu* Gauld, 1985) attack Geometridae, Lasiocampidae and Saturniidae (Gauld & Mitchell, 1977, 1981; Gauld, 1988; Janzen & Gauld, 1997; host records in Janzen & Hallwachs, 2003). This suggests to us that the base of the *Thyreodon* species-group clade may have been a parasitoid of a caterpillar within the Noctuoidea.

Clearly the *Thyreodon* genus-group is a lineage of Ophioninae that specializes in attacking large to very large bombycoid (*sensu* Scoble, 1992) caterpillars (Table 2). The most basal lineage, *Euryophion*, comprises a group of Old World species that are known to parasitize only species of Saturniidae and Eupt-



erotidae, although many species of sphingids occur in the same general region (Kitching & Cadiou, 2000). All members of the other genera are parasitoids of Sphingidae (Table 2), except that the derived *Thyreodon santarosae* parasitizes the larvae of ceratocampine Saturniidae. At present we cannot state whether the genus-group originally attacked saturniids and then switched to sphingids in the *Rhynchophion* + (*Dictyonotus* + *Thyreodon*) clade, or arose on sphingids with the *Euryophion* clade subsequently specializing on saturniids. Both are equally parsimonious suggestions that posit a single host family switch.

The more basal members of the sphingid parasitizing clade, *Rhynchophion* and *Dictyonotus*, predominantly attack hawkmoth caterpillars of the subfamilies Sphinginae and Smerinthinae, as does the temperate North American *Thyreodon atricolor*. One Asian species of *Dictyonotus* also has been reared from a species of the sphingid subfamily Macroglossinae. The majority of species of *Thyreodon* that have been reared in the Neotropics are parasitoids of Macroglossinae, including the more basal taxa, such as *T. woodleyi* (Fig. 66), suggesting that the *Thyreodon* lineage diversified while being macroglossine specialists. The most basal and isolated taxon, *T. woodleyi*, attacks a taxonomically isolated macroglossine belonging to the Philampelini, whereas the most derived *T. atriventris* species-group are restricted to the Dilophonotini, as is *T. erythrocerata*. The most utilized hosts belong to the Macroglossini. Thus the most parsimonious interpretation of these data is that Macroglossini are original hosts of most *Thyreodon*, and some lineages have then specialized on other tribes. The most striking exception is *T. santarosae*, which has switched to ceratocampine saturniids. Although it is possible that this host switch was facilitated by the fact that these large saturniids make a pupation retreat in the soil surface and litter, like that of macroglossine sphingids, but unlike cocoon-spinning saturniine and hemileucine Saturniidae, factors may also be involved, such as the morphological similarity and size of their saturniid larval hosts to sphingid larvae. It is noteworthy that the koinobiont larval endoparasitoid *Cryptophion* lineage has made exactly the same host switch, but these small ichneumonids attack early instar larvae, which they kill on the host larval food plant leaf, and thus do not avail themselves of the shelter of the host's pupation retreat (Gauld & Janzen, 1994).

Of the 23 species of *Rhynchophion* (two) and *Thyreodon* (21) known from Costa Rica, the most thoroughly collected of all the neotropical regions, 21 (91%) have been found in the ACG. Fourteen of these (67%) have now been reared in the ACG. Of the seven present in the ACG, but remaining to be reared, all but one occur

in intermediate-elevation rain forest (or on its interface with dry forest). The single missing dry forest species, *T. rivinae*, has a likely candidate host. Four of the 21 ACG species are known only from rearing, never having been caught in the wild (and many others are known from only a very few wild-caught specimens). The implication is that when all potential hosts have been reared in large numbers in Costa Rica, a few more Costa Rican species may emerge. Although Malaise traps do yield a very few *Rhynchophion* and *Thyreodon* specimens, the bulk of the species are only very rarely or never captured by Malaise traps; most pinned museum specimens have been caught with nets (Table 1). Equally, although *T. atriventris*, *T. rufothorax*, *T. santarosae* and *T. rivinae* come frequently to lights in the early rainy season in the ACG dry forest, the remaining species only very rarely arrive at lights.

Is wild-capture alone sufficient to locate the *Rhynchophion* and *Thyreodon* wasp fauna of Costa Rica? Many hundreds of Malaise-trap years scattered over virtually all Costa Rican habitats and ecosystems during the past 23 years, combined with many miscellaneous net collecting and light collecting of these very large and charismatic wasps, has located 83% of the known fauna. Caterpillar rearing in just the ACG to date has located only 67% of the fauna. However, by the time that the much more labour-intensive rearing programme is finished, it will have located at least 91% of the fauna known today, because 21 species are known to occur in the ACG. However, this rearing programme may well expose yet more species, given that each of the unreared species are known from only a very few specimens.

This first sketch of the hosts and localities of *Rhynchophion* and *Thyreodon* in the ACG yields a blurry image roughly as follows. *T. atriventris* and *T. rufothorax* occur throughout both the dry forest and the rain forest of the ACG (and the remainder of Costa Rica as well), feeding on *Pachylia ficus* and *Pachylia syces*, and on *Pachyloides resumens* and *Pachygonidia drucei*, respectively. All four of these hosts are widespread species of sphingids. Five of the ichneumonid species, *T. santarosae*, *T. maculipennis*, *T. woodleyi*, *R. flammipennis* and *T. rivinae*, are basically dry forest insects, both in Costa Rica and further afield, from the US/Mexico southwards. One of these – *T. santarosae* – has evolved out of Sphingidae and on to ceratocampine Saturniidae. The remaining *Thyreodon* species are restricted to the ACG rain forest and its interface with dry forest, at intermediate elevations (500–1100 m), irrespective of whether they are restricted to the ACG or are more widespread. The rain forest sphingid and saturniid species reared to date in the ACG have not been reared in sufficiently large numbers (7000+ rearings of 79 species from rain

forest and lower margin cloud forest) for us to feel confident that the 'missing' hosts for seven species of *Thyreodon* (Table 1) are not among them. In comparison, 33 000+ individual rearings of 64 potential host species have been made in dry forest.

Species of *Thyreodon* are only very lightly parasitized (its hosts, hyperparasitized), and then only by the large ichneumonid *Cidaphus rostratus* (reared only from two species of *Thyreodon*) (three of 334 wasp rearings, or <1%). However, it is possible that had those caterpillars parasitized by *Thyreodon* been allowed to live out their lives exposed to the hyperparasitoid (rather than sequestered in plastic bags after capture), more of them would have been hyperparasitized.

### ACKNOWLEDGEMENTS

We especially thank Ian Kitching for an interesting discussion on the phylogeny of Sphingidae. This study was supported most recently by NSF grants (D.H.J.) DEB 97050732 and DEB 0072730. We wish to thank the following for caterpillar hunting and husbandry: W. Hallwachs, R. Moraga, G. Sihezar, G. Pereira, L. Rios, M. Pereira, O. Espinosa, E. Cantillano, M. Pereira, R. Franco, J. Perez, H. Ramirez, F. Chavarria, M. M. Chavarria, E. Olson, C. Moraga, P. Ríos, C. Cano, D. Garcia, F. Quesada, E. Araya, E. Guadamuz, R. Espinosa, R. Blanco, A. Guadamuz, D. Perez, R. Blanco, C. Camargo, A. Masis, and W. Haber. We thank Sondra Ward for preparing the SEM photographs and Harry Taylor for producing the colour plates.

### REFERENCES

- Ashmead WH. 1894.** Some Parasitic Hymenoptera from Lower California, Mexico. *Proceedings of the California Academy of Sciences* **2**: 122–129.
- Ashmead WH. 1900a.** Classification of the ichneumon flies, or the superfamily Ichneumonoidea. *Proceedings of the United States National Museum* **23**: 1–220.
- Ashmead WH. 1900b.** Report upon the Aculeate Hymenoptera of the Islands of St Vincent and Grenada, with additions to the Parasitic Hymenoptera and a list of the described Hymenoptera of the West Indies. *Transactions of the Entomological Society of London* **1900**: 207–367.
- Brullé A. 1846.** Hyménoptères. In: Lepeletier de Saint-Fargeau A. ed. *Histoire Naturelle des Insectes* 4, vii+680 pp.
- Burns JM, Janzen DH. 2001.** Biodiversity of pyrrophygine skipper butterflies (Hesperiidae) in the Area de Conservacion Guanacaste, Costa Rica. *Journal of the Lepidopterist's Society* **55**: 15–43.
- Cameron P. 1886.** *Biologia Centrali Americana*. Insecta Hymenoptera (Families Tenthredinidae – Chrysididae). **1**: 241–328.
- Carlson RW. 1979.** Ichneumonidae. In: Krombein KV, Hurd PD, Smith DR, Burks BD, eds. *Catalog of Hymenoptera in America north of Mexico*. Washington DC: Smithsonian Institution Press, 315–740.
- Cresson ET. 1874.** Descriptions of Mexican Ichneumonidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* **1873**: 374–413.
- Cushman RA. 1947.** Generic revision of the Ichneumon-flies of the tribe Ophionini. *Proceedings of the United States National Museum* **96**: 417–482.
- D'Abrera B. 1986.** *Sphingidae Mundi*. Faringdon, UK: E. W. Classey, Ltd.
- Dalla Torre CG. 1901.** *Catalogus Hymenopterorum* 3. Leipzig: Engelmann.
- Enderlein G. 1912.** Beiträge zur Kenntnis aussereuropäischer Ichneumoniden II. Ophioniden. Der Gattung *Thyreodon* und ihr Verwandten. *Zoologischer Anzeiger* **39**: 624–632.
- Gauld ID. 1985.** The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)* **51**: 61–185.
- Gauld ID. 1988.** A survey of the Ophioninae (Hymenoptera: Ichneumonidae) of tropical Mesoamerica with special reference to the fauna of Costa Rica. *Bulletin of the British Museum (Natural History) (Entomology)* **57**: 1–309.
- Gauld ID, Janzen DH. 1994.** The classification, evolution and biology of the Costa Rican species of *Cryptophion* (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society* **110**: 297–324.
- Gauld ID, Mitchell PA. 1977.** *The taxonomy, distribution and host preferences of African parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae)*. Slough, UK: CAB.
- Gauld ID, Mitchell PA. 1981.** *The taxonomy, distribution and host preferences of Indo Papuan parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae)*. Slough, UK: CAB.
- Goloboff PA. 1999.** *NONA*, Version 2.0. Program and documentation. Tucumán, Argentina: Published by the author.
- Hanson PE, Gauld ID, eds. 1995.** *The Hymenoptera of Costa Rica*. Oxford: Oxford University Press.
- Harris AC. 1987.** Pompilidae (Insecta: Hymenoptera). *Fauna of New Zealand* **21**: 1–154.
- Hirayama S. 1941.** *Illustrated thousand insects of Japan in colour*. Tokyo: Sansendo.
- Hooker CH. 1912.** The ichneumon flies of America belonging to the tribe Ophionini. *Transactions of the American Entomological Society* **38**: 1–176.
- Janzen DH. 1984.** Weather-related color polymorphism of *Rothschildia lebeau* (Saturniidae). *Bulletin of the Entomological Society of America* **30**: 16–20.
- Janzen DH. 1993.** Caterpillar seasonality in a Costa Rican dry forest. In: Stamp NE, Casey TM, eds. *Caterpillars. Ecological and evolutionary constraints on foraging*. New York: Chapman & Hall, 448–477.
- Janzen DH. 2002.** Tropical dry forest: Area de Conservacion Guanacaste, northwestern Costa Rica. In: Perrow MR, Davy AJ, eds. *Handbook of ecological restoration, vol. 2: restoration in practice*. Cambridge, UK: Cambridge University Press, 559–583.

- Janzen DH. 2003.** How polyphagous are Costa Rican dry forest saturniid caterpillars? In: Basset Y, Novotnyh V, Miller SE, Kitching RL, eds. *Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy*. Cambridge, UK: Cambridge University Press, 369–379.
- Janzen DH, Gauld ID. 1997.** Patterns of use of large moth caterpillars (Lepidoptera: Saturniidae and Sphingidae) by ichneumonid parasitoids (Hymenoptera) in Costa Rican dry forests. In: Watt AD, Stork NE, Hunter MD, eds. *Forests and insects*. London: Chapman & Hall, 251–271.
- Janzen DH, Hallwachs W. 2003.** *Philosophy, navigation and use of a dynamic database (ACG Caterpillars SRNP) for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica*. <http://janzen.sas.upenn.edu>.
- Janzen DH, Walker AK, Whitfield JB, Delvare G, Gauld ID. 2003.** Host-specificity and hyperparasitoids of three new Costa Rican species of *Microplitis* Foerster (Hymenoptera: Braconidae: Microgastrinae), parasitoids of sphingid caterpillars. *Journal of Hymenoptera Research* **12**: 42–76.
- Kester K, Tuttle J. 1999.** Host identified for *Rhynchophion flammipennis* (Hymenoptera: Ichneumonidae). *Southwestern Naturalist* **44**: 87–88.
- Kettlewell HBD. 1963.** The genetical and environmental factors which affect colour and pattern in Lepidoptera, with special reference to migratory species. *Entomologist* **96**: 127–130.
- Kitching IJ, Cadiou J-M. 2000.** *Hawkmoths of the world*. Cornell: Cornell University Press.
- Morley C. 1912.** *A revision of the Ichneumonidae*. London: Trustees of the British Museum.
- Morley C. 1926.** On some South African Ichneumonidae in the collection of the south. *African Museum* **23**: 435–481.
- Nixon K. 2000.** WINCLADA (Beta), Version 0.0.99m10.1. Ithaca, NY: Published by the author.
- Peigler RS. 1994.** Catalog of parasitoids of Saturniidae of the World. *Journal of Research on the Lepidoptera* **33**: 1–121.
- Porter CC. 1976.** New records for *Thyreodon* from South Texas. *Psyche* **83**: 304–309.
- Porter CC. 1980.** A new *Thyreodon* Brullé (Hymenoptera: Ichneumonidae) from South Texas. *Florida Entomologist* **63**: 242–246.
- Porter CC. 1984.** *Laticinctus* group *Thyreodon* in the northern Neotropics (Hymenoptera: Ichneumonidae). *Wasmann Journal of Biology* **42**: 40–71.
- Porter CC. 1986.** A new arboricolous *Thyreodon* from Costa Rica (Hymenoptera: Ichneumonidae: Ophioninae). *Psyche* **93**: 133–139.
- Porter CC. 1989.** A new Floridan *Athyreodon* Ashmead (Hymenoptera: Ichneumonidae) with comments on related species of the northern Neotropics. *Florida Entomologist* **72**: 294–304.
- Schauff ME, Janzen DH. 2001.** Taxonomy and ecology of Costa Rican *Euplectrus* (Hymenoptera: Eulophidae), parasitoids of caterpillars (Lepidoptera). *Journal of Hymenoptera Research* **10**: 181–230.
- Schulz WA. 1903.** Ueber *Tipulophion rufithorax* Cameron (Hymenoptera). *Zeitschrift für Systematische Hymenopterologie und Dipterologie* **3**: 249–253.
- Scoble MJ. 1992.** *The Lepidoptera*. Oxford: Natural History Museum and Oxford University Press.
- Shestakov A. 1926.** *Tabula diagnostica et species palaearticae*. *Konowia* **5**: 256–263.
- Sime KR, Wahl DB. 2002.** The cladistics and biology of the *Callojoppa* genus-group (Hymenoptera: Ichneumonidae, Ichneumoninae). *Zoological Journal of the Linnean Society* **134**: 1–56.
- Smith F. 1879.** *Descriptions of new species of Hymenoptera in the collections of the British Museum*. London: British Museum.
- Szépligeti GV. 1905.** Hymenoptera, Ichneumonidae. In: Wytsman P. *Genera Insectorum* **34**: 1–68.
- Szépligeti GV. 1906.** Neue exotische Ichneumoniden aus der Sammlung des Ungarischen National-Museums. *Annales Musei Nationalis Hungarici* **4**: 119–156.
- Townes HK. 1945.** A catalogue and reclassification of the Nearctic Ichneumonidae (Hymenoptera). Part II, The subfamilies Mesoleiinae, Plectiscinae, Orthocentrinae, Diplazontinae, Metopiinae, Ophioninae, Mesochorinae. *Memoirs of the American Entomological Society* **11**: 478–925.
- Townes H. 1963.** Evidence among the ephialtine Ichneumonidae for a Bering migration route. In: *Pacific Basin biogeography, a symposium*. Honolulu, HI: Bishop Museum Press, 153–158.
- Townes H. 1971.** Genera of Ichneumonidae, Part 4. *Memoirs of the American Entomological Institute* **17**: 1–372.
- Townes H, Townes M. 1966.** A catalogue and reclassification of Neotropical Ichneumonidae. *Memoirs of the American Entomological Institute* **8**: 1–367.
- Uchida T. 1928.** Zweiter Beiträge zur Ichneumoniden Fauna Japans. *Journal of the Faculty of Agriculture of Hokkaido Imperial University* **21**: 177–297.
- Vardy CR. 2000.** The New World tarantula-hawk wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae). Part 1. Introduction and the *P. rubra* species-group. *Zoologische Verhandlungen* **332**: 1–86.

## APPENDIX 1

1. *Mandibular axis*: (0) more less horizontal, thus at 90° to longest axis of head; (1) inclined at about 45° to longest axis of head.
2. *Mandible, form of*: (0) moderately long, evenly tapered and not twisted; (1) slender and twisted.
3. *Labrum*: (0) exposed; (1) concealed.
4. *Mouthparts*: (0) unspecialized; (1) elongated.
5. *Maxillary palpomere II of female*: (0) cylindrical or very slightly inflated; (2) grossly inflated and often slightly flattened.
6. *Clypeus, with margin*: (0) weakly convex, thin; (1) sharp, rounded to pointed and flared outwards; (2) blunt and weakly concave.



7. *Malar space*: (0) more or less occluded; (1) about 0.3–0.5 times basal mandibular width; (2) >0.8 times basal mandibular width.
8. *Lower face centrally*: (0) punctate; (1) coriaceous to rugose.
9. *Frons laterally*: (0) simple; (1) with a sharp carina close to and parallel with margin of eye.
10. *Frons, between antennal sockets*: (0) simple; (1) with raised parallel ridges; (2) with a median protuberance; (3) with a single median vertical carina.
11. *Ocelli, size of posterior ones*: (0) large, more or less contiguous with eye; (1) moderate sized, separated from eye by about 0.5 their own diameter or less; (2) small, separated from eye by more than their own diameter.
12. *Lower end of occipital carina*: (0) evanescent before reaching hypostomal carina; (1) joining hypostomal carina.
13. *Central flagellomeres*: (0) elongate; (1) subquadrate to transverse.
14. *Apical flagellomeres*: (0) with short bristles; (1) with bristles that are longer than the diameter of the flagellomere.
15. *Colour of antenna of female*: (0) yellowish brown; (1) blackish; (2) bright yellow; (3) yellow/white with apex black.
16. *Face of male*: (0) concolorous with female; (1) contrasting with that of female.
17. *Hind margin of pronotum mediodorsally*: (0) unspecialized; (1) thickened and subquadrate in profile; (2) thickened and with upper anterior margin projecting strongly forwards.
18. *Anterior margin of pronotum*: (0) flat; (1) thickened and upturned centrally; (2) strongly reflexed, the reflexed part very broad.
19. *Lower hind corner of propleuron*: (0) simple; (1) expanded and impressed
20. *Mesoscutum with median and lateral lobes*: (0) finely and sparsely punctate; (1) coarsely but sparsely punctate; (2) very closely punctate, the punctures separated by less than their own diameters.
21. *Notaulus, length of*: (0) weakly and shallowly impressed anteriorly; (1) more sharply impressed and reaching beyond centre of mesoscutum.
22. *Notaulus, sculpture of*: (0) smooth; (1) transversely striate; (2) coarsely coriaceous to rugose; (3) foveolate.
23. *Anterior part of notaulus*: (0) unspecialized; (1) with inner margin raised to form a longitudinal ridge; (2) with a strong transverse crest.
24. *Lateral carina of scuto-scutellar groove*: (0) simple; (1) flattened and laterally projecting.
25. *Mesopleuron with speculum*: (0) almost smooth and confined to upper hind corner; (1) extensive, reaching forwards; (2) sculptured and more or less indistinguishable.
26. *Sculpture of lower part of mesopleuron*: (0) finely punctate; (1) coarsely punctate; (2) smooth and impunctate.
27. *Supra-sternular sculpture band*: (0) absent; (1) vestigial but discernible; (2) strong and deeply foveolate.
28. *Sternaulus*: (0) absent or discernible as a shallow but otherwise undifferentiated depression; (1) present as a distinct impression and/or sculpturally differentiated area.
29. *Epicnemial carina*: (0) with upper end extending about 0.5 of way up pleuron; (1) present only ventrally; (2) with upper end curved backwards and down.
30. *Posterior transverse carina of mesosternal region*: (0) absent or incomplete; (1) complete.
31. *Hind margin of metanotum*: (0) unspecialized; (1) with a large lateral swelling.
32. *Lateral part of metanotum*: (0) simple; (1) swollen and carinate.
33. *Metapleuron*: (0) finely and sparsely punctate; (1) closely and coarsely punctate; (2) coriaceous/rugulose.
34. *Metapleural boss*: (0) absent; (1) present.
35. *Anterior margin of propodeum*: (0) with a shallow transverse groove that is partially obscured sublaterally and with a median semicircular concavity centrally; (1) with a very deeply impressed, U-shaped groove.
36. *Propodeal spiracle*: (0) elliptical; (1) elongately linear.
37. *Propodeum in profile*: (0) of normal size, not overhanging metapleuron (Fig. 32); (1) grossly inflated to overhang reduced metapleuron (Figs 27–31).
38. *Propodeum anteromedially*: (0) simple; (1) with an anteromedian tubercle.
39. *Propodeum with anterior transverse carina*: (0) present; (1) vestigial or absent.
40. *Propodeum with posterior transverse carina*: (0) present; (1) vestigial or absent.
41. *Propodeal sculpture pattern*: (0) with weak coriaceous sculpture; (1) coarsely rugose-coriaceous; (2) coarsely reticulate; (3) smooth and very sparsely punctate; (4) striate; (5) finely reticulate; (6) closely and coarsely punctate.
42. *Propodeum posteriorly, mediodorsally*: (0) more or less flat; (1) with a shallow median longitudinal furrow; (2) with a deep median longitudinal impression.
43. *Propodeum with lateromedian furrows*: (0) absent; (1) present.
44. *Propodeum above and behind spiracle*: (0) unspecialized; (1) with a longitudinal polished tubercle; (2) with a large flange.

45. *Mesosoma colour*: (0) orange-brown; (1) blackish; (2) metallic blue.
46. *Fore tibial spur membrane*: (0) complete; (1) present only as basal vestige.
47. *Fore leg of ♀ with length of 5th tarsomere in comparison with 3rd + 4th*: (0) conspicuously shorter, <0.7 times as long; (1) 0.8 times as long or longer.
48. *Hind coxa*: (0) moderately large, its apex projecting beyond hind margin of propodeum; (1) small, its apex more or less level with hind margin of propodeum.
49. *Hind coxa colour*: (0) orange-brown; (1) black.
50. *Hind femur of ♀*: (0) slender and subcylindrical; (1) stout and laterally compressed.
51. *Hind tarsal claws of ♀*: (0) evenly curved; (1) very long and weakly curved.
52. *Hind tarsus of ♂ ventrally*: (0) finely and sparsely pubescent; (1) with moderately long, dense pubescence; (2) with exceptionally long pubescence.
53. *Fore wing*: (0) hyaline; (1) extensively dark; (2) dark with centre subhyaline; (3) variegated, i.e. hyaline with a few dark marks.
54. *Fore wing with anterior corner of discosubmarginal cell*: (0) with a small glabrous area; (1) without any trace of a glabrous area.
55. *Fore wing with base of Rs + 2r-rs*: (0) slender; (1) thickened and abruptly curved before joining pterostigma.
56. *Fore wing with 3rs-m*: (0) slightly shorter than abscissa of *M* between *2m-cu* and *3rs-m*; (1) longer than abscissa of *M* between *2m-cu* and *3rs-m*.
57. *Fore wing with abscissa of 1m-cu distal to bulla*: (0) longer than abscissa of *M* between *2m-cu* and *3rs-m*; (1) slightly shorter than abscissa of *M* between *2m-cu* and *3rs-m*.
58. *Pterostigma*: (0) of moderate breadth; (1) very slender (as in Figs 7–14).
59. *Fore wing with abscissa of Cu1a between Cu1b and 2m-cu*: (0) clearly longer than abscissa of *Cu1* between *cu-a* and *1m-cu*; (1) shorter than abscissa of *Cu1* between *cu-a* and *1m-cu*.
60. *Hind wing with rs-m*: (0) straight; (1) bowed.
61. *Hind wing, proximal end of marginal cell*: (0) finely and sparsely hirsute, the membrane not thickened; (1) glabrous with membrane thickened.
62. *Hind wing with basal hamuli*: (0) present; (1) absent.
63. *Hind wing with distal abscissa of Cu1*: (0) intermediate between *M* and *1A* or closer to *1A*; (1) closer to *M*.
64. *Metasoma colour*: (0) orange-brown; (1) blackish; (2) metallic blue; (3) blackish with yellow median band.
65. *Tergite II with thyridium*: (0) elliptical and close to anterior margin; (1) subcircular, remote from anterior margin; (2) absent.
66. *Tergite II with laterotergite*: (0) folded up, inconspicuous; (1) pendant, large.
67. *Tergite II length*: (0) slightly longer than tergite III; (1) very conspicuously shorter than tergite III.
68. *Dorsal margin of clasper*: (0) simple; (1) notched.
69. *Apex of clasper*: (0) rounded to obliquely truncated; (1) with a small dorsal protuberance; (2) with a spine-like dorsal protuberance.
70. *Ventral apex of clasper*: (0) rounded to truncated; (1) with a small ventral protuberance.
71. *Apex of aedeagus*: (0) convex; (1) flattened.
72. *Subapex of aedeagus laterally*: (0) unspecialized; (1) with a sharp lateral keel.
73. *Male subgenital plate*: (0) slightly elongate, posteriorly convex; (1) strongly transverse, posteriorly slightly concave.