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First host records for the rogadine genera *Rogasodes* Chen and He and *Canalirogas* van Achterberg and Chen (Hymenoptera: Braconidae) with description of a new species and survey of mummy types within Rogadinae s. str.

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Abstract

The parasitic wasp genus *Rogasodes* is recorded for the first time outside mainland China, based on a new species, *R. scytalopatericola* Quicke and Shaw sp. nov., from Java. Rearing data and host remains associated with the type specimen show that it is a parasitoid of the palm-feeding drepanid moth, *Scytalopteryx elongata* (Snellen). *Canalirogas* sp. aff. *balgooyi* van Achterberg and Chen is recorded from an unidentified lymantriid on clove trees in Indonesia (Sumatra) and illustrated. Both of these are the first host records for the genera. *Rogas spilonotus* Cameron is transferred to *Canalirogas*. A survey of mummy sclerotization and adult emergence holes in the subfamily Rogadinae *sensu stricto* is presented. The data suggest an early shift to a posterior emergence position, with a strictly dorsal position being largely characteristic of the common genus *Aleiodes*. Only *Aleiodes* and a few apparently closely related taxa, including *Hemigyroneuron*, typically form heavily sclerotized mummies.

Keywords: Aleiodes, balgooyi, Hemigyroneuron, *host relationships, Rogadinae,* Rectivena, Rogas, Rogasella, spilonotus, *systematics,* Yelicones

Introduction

The rogadine braconid genus *Rogasodes* Chen and He was recently described on the basis of a single species from China (Chen and He 1997) though its biology has remained unknown. All Rogadinae *sensu stricto* (i.e. comprising Clinocentrini, Stiropiini, Yeliconini, and Rogadini) are koinobiont endoparasitoids of Lepidoptera larvae, which they "mummify" before pupating inside this modified host structure. The Rogadini is dominated by the cosmopolitan genus *Aleiodes* Wesmael, members of which attack a wide range of lepidopteran families (Shaw MR 1983, 1994, 2003; Shaw SR 1997; Shaw and

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Huddleston 1991; Fortier and Shaw 1999), but it also includes another group of genera, including *Canalirogas* van Achterberg and Chen, that appears to be monophyletic on the basis of molecular (Chen et al. 2003; M. Mori and D. L. J. Quicke, unpublished observations) and morphological (Zaldivar-Riveron et al. 2004) analyses. Adult and mummy features suggest that *Rogasodes* may belong to this other clade.

The posteroventral position of the parasitoid's emergence hole and the very thin mummy made by the new species differs markedly from the typically very hard and heavily tanned mummies made by *Aleiodes* species, with strictly posterodorsal emergence, and prompted us to examine the distribution of emergence hole positions and mummy type throughout the subfamily and to consider the results in the light of the emerging picture of rogadine phylogenetic relations based on internal morphology and DNA studies.

Terminology

Terminology follows van Achterberg (1979, 1988). Descriptions of sculpture follow Harris (1979). Measurements of the height and horizontal length of the eye are approximations because the very bulbous face and very large eyes make it difficult to measure consistently; in our attempts to do so, the head was orientated so that the face (defined as running from the anterior edge of the toruli to the dorsal margin of the clypeus) was horizontal or perpendicular to the measurement axis.

The following abbreviations are used: NHM (The Natural History Museum, London); USNM (United States National Museum, Washington, DC).

Systematics

Rogasodes Chen and He

Rogasodes Chen and He 1997, p 88–89.

Previously known only from the type species, *Rogasodes masaicus* Chen and He; a second species, described below, can be separated using the following key.

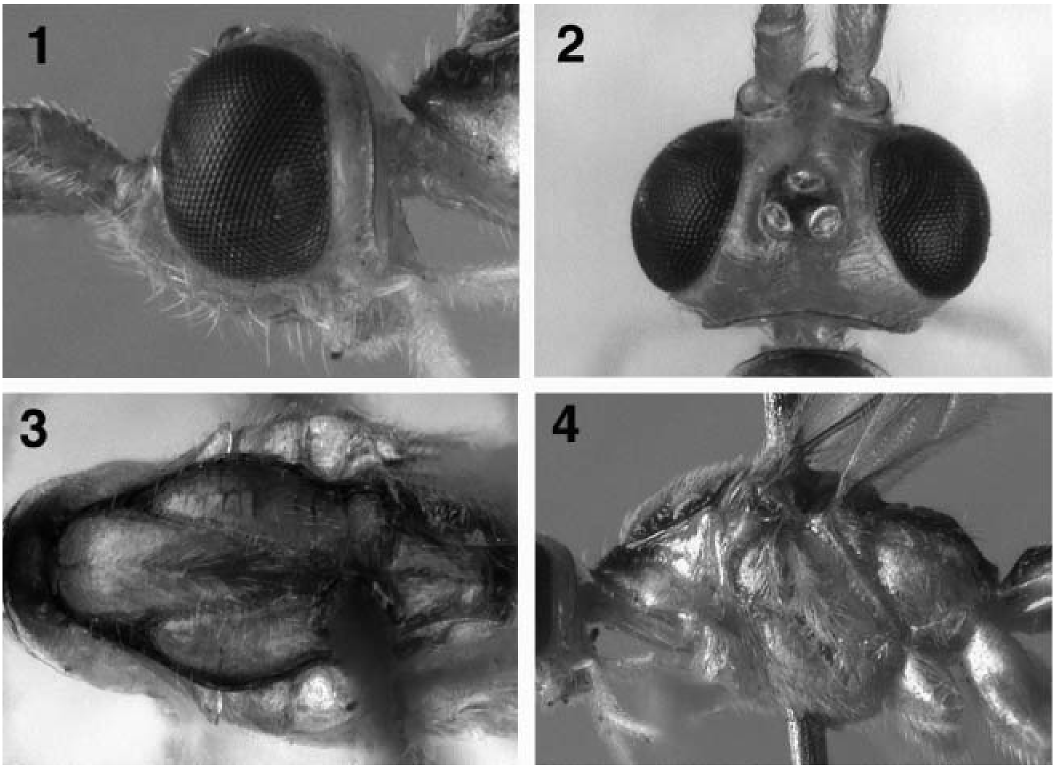
1. Fore wing vein cu-a interstitial (Figure 9); second metasomal tergite less than 1.7 times longer than third medially; pterostigma uniformly dirty yellow; mesopleuron and mesosternum pale yellow-brown. . . . . *scytalopptericola* sp. nov.
– Fore wing vein cu-a postfurcal to vein 1-M by approximately three vein widths; second metasomal tergite more than 1.8 times longer than third medially; pterostigma brown with extreme apex yellow; mesopleuron (except spectrum) and mesosternum pitchy brown . . . . *masaicus* Chen and He

Description of new species

Rogasodes scytalopptericola sp. nov. Quicke and Shaw

(Figures 1–7, 9)

Holotype: female, "Ex [indecipherable] *Phyllopteryx elongata* Sn. leg. R. Awilowo, Keboeme [indecipherable], (N. Java) iv.1933 I.v Pl.", "Ex. Caterp. *Phyllopteryx elongata*, Leg. R. Awilowo. Keboemen. IV-'33. I.v Pl". ["I.v Pl" printed on both labels and appears

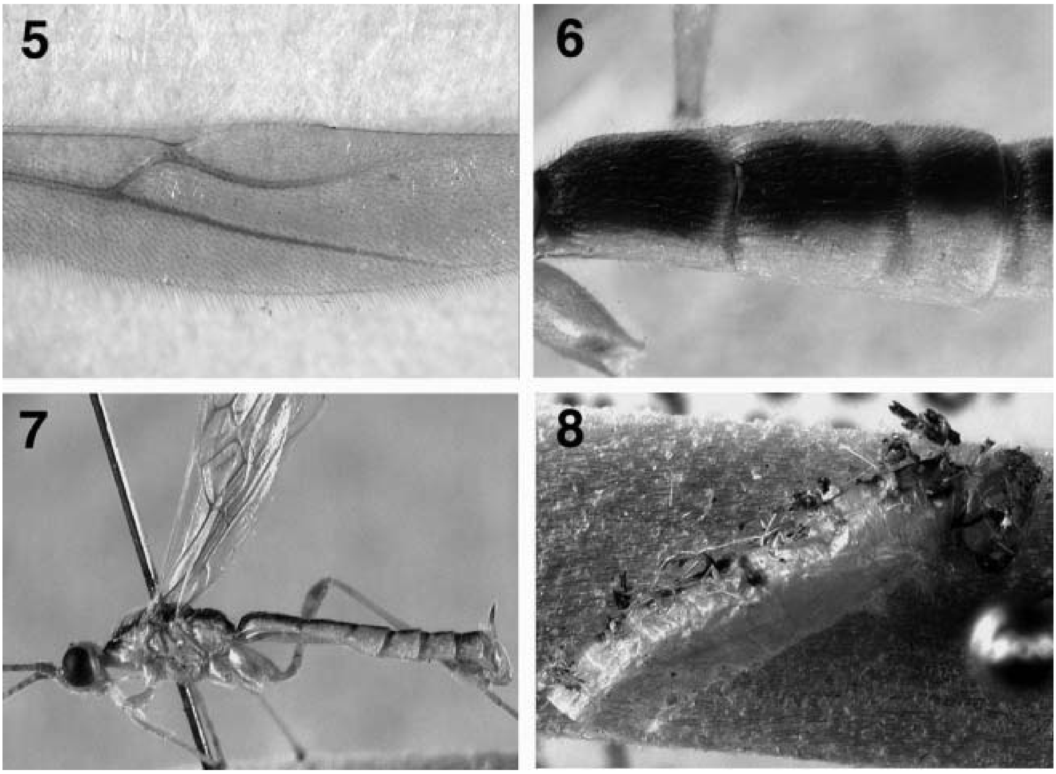


Figures 1–4. *Rogasodes scytalopptericola* sp. nov., Automontage® light micrographs. (1) Head, lateral aspect. (2) Head, dorsal aspect. (3) Pronotum, mesoscutum and scutellum, dorsal aspect. (4) Mesosoma, lateral aspect.

to refer to a person's collection], and "101". Mounted on micropin on same mount as mummified host remains, which are missing some posterior segments (USNM).

Lengths. Length of body 5.8 mm; length of fore wing 4.25 mm.

Head (Figures 1, 2). Antenna with >35 flagellomeres (incomplete in available female specimen); with long setosity. Median flagellomeres oblique in lateral view, 2.8 times longer maximally than wide. Basal flagellomere 4.1 times longer than wide, rather oblique apically, 1.7 and 1.9 times longer than second and third, respectively. Third flagellomere 2.2 times longer than wide. Face strongly protruding. Height of clypeus: inter-tentorial distance: tentorio-ocular distance = 1.0:3.4:1.6. Head short, 1.5 times wider than maximally long in dorsal view (length measured from occipital carina to front of face). Width of head 2.4 times shortest distance between eyes. Eyes very large, strongly emarginate. Height of eye 1.3 times shortest distance between eyes. Horizontal length of eye (in dorsal view, perpendicular to face) 4.3 times horizontal length of head behind eye. Frons flat, smooth, with deep mid-longitudinal carina. Posterior ocellar line: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 1.0:2.25:2.25. Head strongly narrowed behind eyes. Occiput largely smooth and shiny with weak transverse punctate striations. Occipital carina strong, forming a laterally protruding flange; with some crenulation next to it on its lower third before it joins hypostomal carina.



Figures 5–8. *Rogasodes scytaloptericola* sp. nov., Automontage® light micrographs. (5) Distal part of hind wing showing thickened vein 1-SR+M and basally curved vein SR. (6) Metasomal tergites 1–3, oblique dorsal aspect. (7) Habitus, lateral aspect. (8) Mummified host remains, posterior segments missing, showing its pale almost transparent nature.

Mesosoma (Figures 3, 4). Mesosoma 1.6 times longer than deep. Pronotum strongly protruding in front of mesoscutum; lateral depressed area coarsely crenulate, finely coriacious-aciculate below this, smooth and shiny posterodorsally. Mesoscutum largely

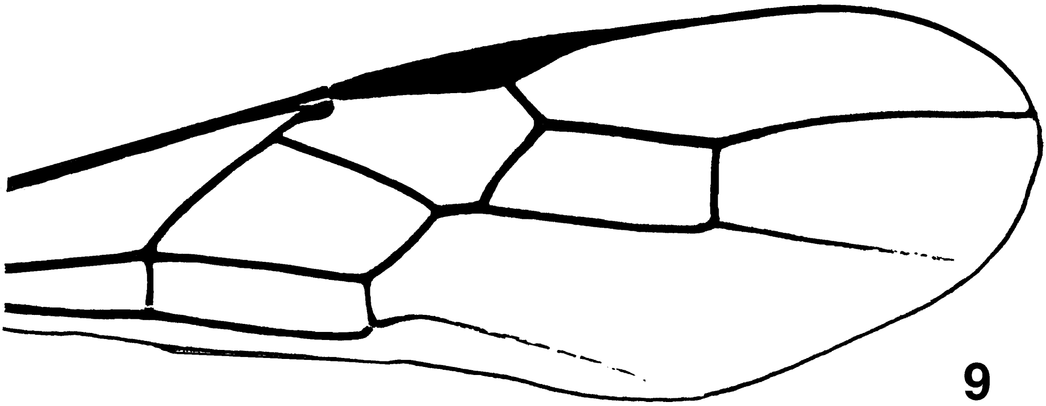


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Figure 9. *Rogasodes scytaloptericola* sp. nov., drawing of fore wing venation showing interstitial vein cu-a. Note: the pterostigma is damaged and therefore the reconstructed image may not be that accurate.

smooth and shiny, with little setosity. Middle lobe of mesoscutum strongly protruding in front of lateral lobes. Notauli strongly impressed and crenulate along whole length; posteriorly merging into a weakly depressed strongly longitudinally striate area. Mesosternum weakly, finely coriaceous. Mesopleuron smooth and shiny; mesopleural sulcus deep and crenulate, sloping ventrally posteriorly. Scutellar sulcus with three carinae between the outer ones. Scutellum smooth and shiny. Propodeum strongly arched in lateral profile; with pair of posteriorly strongly diverging carinae arising near mid-anterior margin; with transverse striae between these anteriorly; medio-posteriorly with several well-developed longitudinal striae.

Wings. Fore wing (Figure 9): length of veins r:3-SR:SR1 = 1.0:3.0:5.9. Vein r-m 0.65 times vein 2-SR. Lengths of veins m-cu:2-SR+M = 2.0:1.0. Vein 1-SR+M very weakly sinuate. Veins 1-M and m-cu weakly curved. Vein cu1b almost absent. Vein cu-a interstitial. Hind wing (Figure 5): vein 2-SR+M interstitial. Vein M+CU 1.1 times length of vein 1-M. Vein m-cu absent.

Legs. Claws with large, acutely pointed basal lobe. Length of fore femur (excluding trochantellus): tibia: tarsus = 1.0:1.17:1.23. Apex of hind tibia with setal comb on inner face. Length of hind femur (excluding trochantellus): tibia: basitarsus = 1.7:1.9:1.0. Hind basitarsus 9.3 times longer than maximally deep.

Metasoma (Figures 6, 7). Metasoma largely strongly longitudinally striate with interspaces coriaceous; with six fully exposed, sculptured tergites. First tergite 1.3 times longer than posteriorly wide; with longitudinal striation and complete strong mid-longitudinal carina. Second metasomal tergite 1.1 times wider posteriorly than medially long; largely finely longitudinally striate, with a well-developed mid-basal triangular area occupying one-third basal width of tergite, and with complete mid-longitudinal carina. Second suture bisinuous. Third tergite 1.9 times wider than medially long. Ovipositor strongly down-curved.

Colour. Largely yellow-brown; antenna becoming somewhat darker distally; stemmaticum, pronotum mid-anteriorly, mesoscutum narrowly laterally, axillary region, propodeum medially, metasomal tergites 1–6 medially, and ovipositor sheaths almost black. Wings hyaline with pale brown venation and dirty yellow pterostigma.

Biology. The single known specimen is mounted with an almost transparent, thinly walled and scarcely tanned mummy of an undoubted drepanid larva (Figure 8), presumed to be the species recorded on the data label that is now known as *Scytalopteryx elongata* (Snellen) (see below). The emergence hole is situated approximately mid-ventrally in the 5th abdominal segment, and the portion of the mummy posterior to that is missing.

Notes. The recorded host, *Phyllopteryx elongata*, is now correctly placed in the genus *Scytalopteryx* Ritsema, 1890, which was created because *Phyllopteryx* Snellen, 1889 was found to be a junior homonym of the sea horse genus, *Phyllopteryx* Swainson, 1839 (Holloway 1998; http://www.mothsofborneo.com/part-8/drepaninae/drepaninae_18_1.php). Van Achterberg (1989) reported that he had seen a specimen of a rogadine reared from *Scytalopteryx* [as *Phyllopteryx*] *elongata* in the collection of the Bogor Institute for Research on Food Crops, Indonesia, which "…most likely belongs to [*Darnilia*]…", a genus described on the basis of a species reared from the limacodid genus *Darna*. It is hard to see how *Darnilia* could be confused with *Rogasodes* as these two genera differ in numerous features including the far shorter hind wing vein M+CU (less than 0.5 times length of 1-M in *Darnilia*), lack of the strongly basally curved hind wing vein SR, and lack of a mid-basal triangular area and mid-longitudinal carina on the 2nd metasomal tergite in *Darnilia* (Chen and He 1997). Therefore it is possible that *Scytalopteryx* is attacked by more than one genus of non-*Aleiodes* Rogadinae.

Placement of the new species in *Rogasodes* requires some discussion. This genus is very similar to *Rogasella* Baker (Baker 1917), currently known only from the Philippines and Indonesia, though the original description of *Rogasodes* (Chen and He 1997) only makes comparisons with two Afrotropical genera because of the availability of a recent key for that region (van Achterberg 1991). These two genera differ in that *Rogasella* has only a minute mid-basal area on the 2nd metasomal tergite and has a longer sclerotized part of hind wing vein SR (C. van Achterberg, personal communication). The new species has a distinct mid-basal area on the 2nd tergite (basally occupying one-third the width of the tergite) though vein SR is tubular for approximately one-quarter of its length. These two genera will probably need to be synonymized when the Indo-Australian Rogadinae are fully revised (C. van Achterberg, in preparation). There are no host records for *Rogasella*.

The new species is also remarkable in that it has fore wing vein cu-a interstitial, a feature that in other rogadines might be taken to be of generic importance. However, as the species is otherwise extremely similar to *R. masaicus* we have no hesitation in including them in the same genus.

The host moth of *Rogasodes scytaloptericola* sp. n., *Scytalopteryx elongata*, is reported as a pest species, having been recorded as attacking two palm genera in South-East Asia, *Cocos* L. and *Elaeis* Jacq. (Arecaceae), and also, more dubiously, *Coffea* L. (Rubiaceae) and *Lablab* Adans. (Fabaceae) (Yunus and Ho 1980), but in the taxonomic literature Holloway (1998) notes that it is rare, having seen only a single individual with precise data. Several related drepanids attack Arecaceae, and whether it is *S. elongata*, or a species whose larva resembles it, that can reach pest status is not clear.

Canalirogas van Achterberg and Chen

Canalirogas van Achterberg and Chen 1996, p 63–65.

First host record for the genus Canalirogas

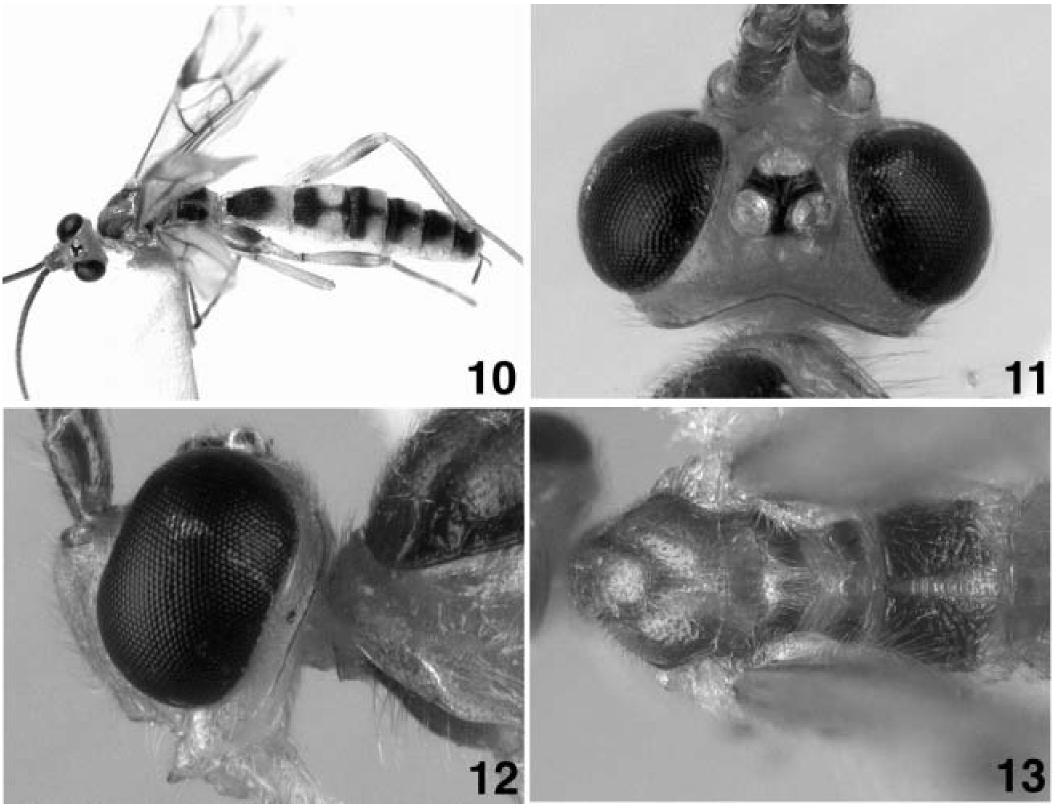
A reared female specimen of *Canalirogas* was located in the NHM bearing the following labels: "N SUMATRA Temburn, Tarokaro XII 1989", "Tube 1. ex Nettle Caterpillar on clove, CIE A20831", "Pres by Comm Inst Ent B.M. 1990-1" and "*Aleiodes spilonotus* (Cameron) det A.K. Walker". Mounted on the same pin, glued to a card, is an emerged rogadine mummy (Figure 28) of an unidentified, strongly ornamented, lymantriid larva (Shen-Horn Yen, personal communication). Although the term nettle caterpillar is usually applied to members of the Limacodidae it may also be applied more loosely to include various spiky or hairy larvae, especially when they are urticating (as are the larvae of many Lymantriidae).

In the key to the 11 known species of *Canalirogas* species by van Achterberg and Chen (1996), the specimen runs to couplet 10 and fairly easily can be run out to *C. balgooyi* van Achterberg and Chen, the type species of the genus, except that it has fairly well-developed antero-lateral convexities on metasomal tergites 3 and 4. We examined the female type specimen of *Aleiodes spilonotus* (Cameron) (NHM; 3.c. 222), the species that the specimen had been identified as, and concur that it is very similar to the reared specimen and also belongs to *Canalirogas*, hence *Canalirogas spilonotus* (Cameron) comb. n. From the large section in van Achterberg and Chen (1996) on the morphological and colour variation observed in *balgooyi*, together with its large geographic range [China, Nepal, India, West Malaysia (the type locality), Borneo Island, Sumatra, and Bali] it is possible that this is a species aggregate rather than a single species, and therefore we choose neither to synonymize *balgooyi* with *spilonotus* nor to state firmly that the specimen dealt with here is indeed either of these nominal species. The reared specimen is illustrated here in Figures 10–17.

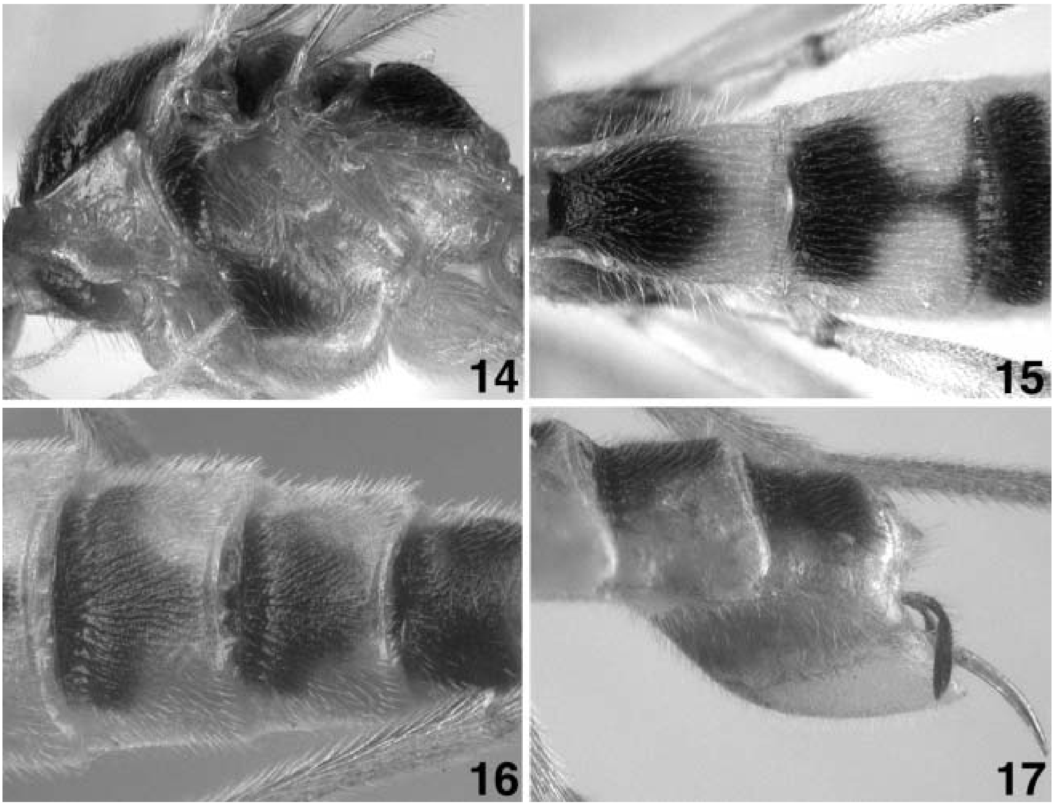
Discussion

Phylogeny and host associations of Rogadini

Recent molecular work (Chen et al. 2003; Zaldivar-Riveron et al. forthcoming; M. Mori and D. L. J. Quicke, unpublished data) suggests that the Rogadini contains two large monophyletic groups, one composed of *Aleiodes* and a few related taxa (e.g. *Arcaleiodes* He and Chen, *Cordylorhogas* van Achterberg, and *Hemigyroneuron* Baker), the other of most other Rogadini genera which we will refer to as the *Rogas* Nees group. These findings are largely in agreement with studies of variation in the venom apparatus (Zaldivar-Riveron et al. 2004) which similarly supported the existence of a monophyletic *Rogas* group, distinct



Figures 10–13. Reared female of *Canalirogas* sp. aff. *balgooyi*, Automontage® light micrographs. (10) Habitus. (11) Head, dorsal view. (12) Head and anterior part of mesosoma, lateral view. (13) Mesosoma, dorsal view.

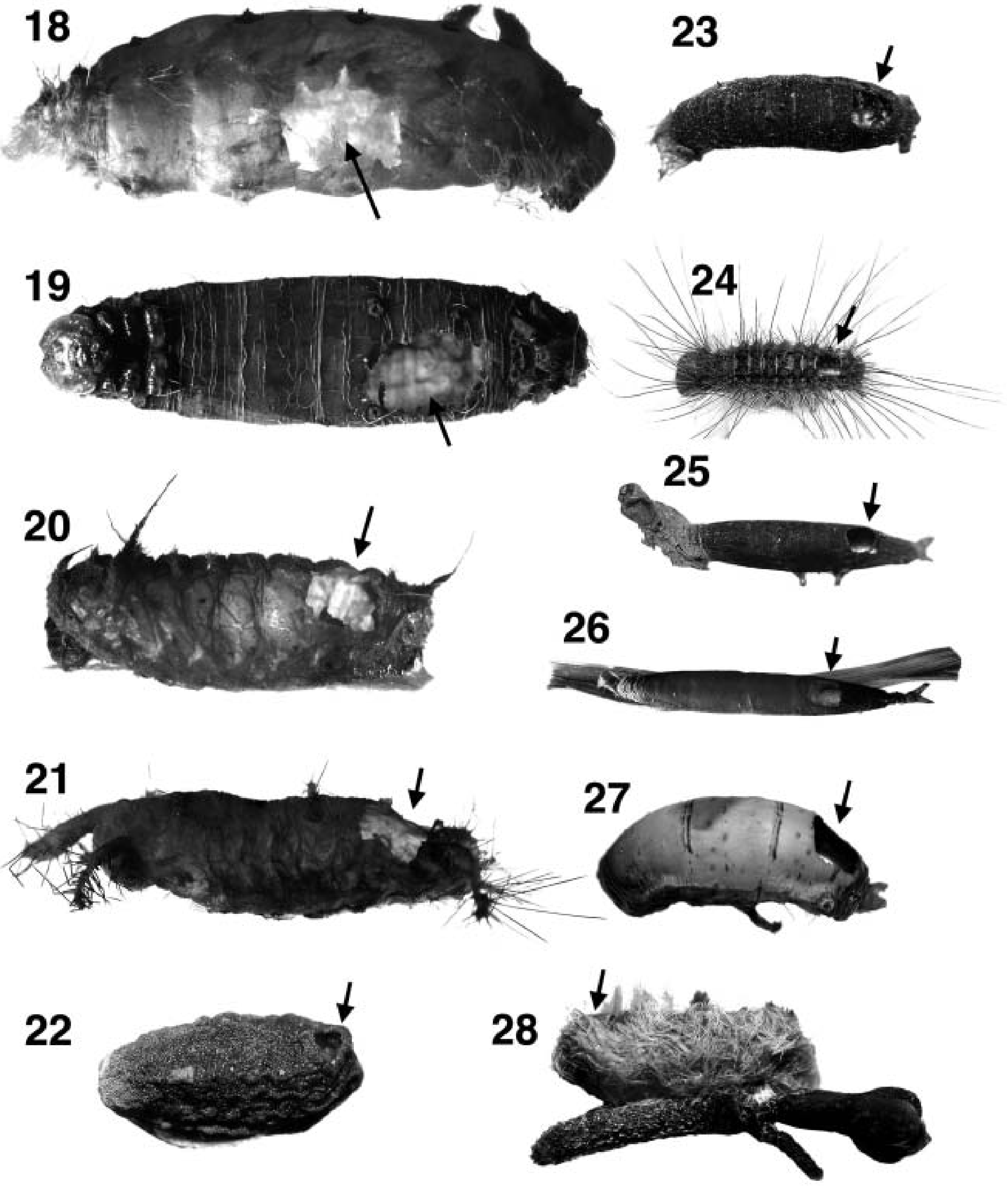


Figures 14–17. Reared female of *Canalirogas* sp. aff. *balgooyi*, Automontage® light micrographs. (14) Mesosoma, lateral view. (15) Metasomal tergites 1–3, dorsal view. (16) Metasomal tergites 4–6, dorsal view. (17) Apex of metasoma, lateral view, showing hypopygium and ovipositor.

from *Aleiodes*, based on the presence in the former of a thickened and secondary venom duct with a flange whereas the *Aleiodes* group is characterized by a soft and recessed secondary duct. Although formal maximum parsimony analysis of venom apparatus features alone did not recover the *Aleiodes* group as monophyletic, the recessed nature of the putative valve connecting the secondary venom duct with the venom reservoir provides a convincing synapomorphy.

Within the *Rogas* group, there appears be a clade comprising several genera with elongate metasomata, most of which also have a sub-basally narrowed first metasomal tergite, a rather large ventrally curved hypopygium, and a down-curved ovipositor: *Colastomion* Baker, *Cystomastax* Szépligeti, *Cystomasticoides* van Achterberg, *Myocron* van Achterberg, *Macrostomion* Szépligeti, and *Megarhogas* Szépligeti. *Canalirogas* is intermediate in that although it has the elongate metasoma (Figure 10), large ventrally curved hypopygium and a down-curved ovipositor (Figure 17), it has the first metasomal tergite not strongly narrowed sub-basally (Figure 15).

Very little is known about the host associations of the members of the *Rogas* group, or indeed of most of the rest of the Rogadini, but what is known is summarized in Table I. Quicke et al. (2003) note that many taxa related to *Rogas* (including the genera of Spinariina: *Spinaria* Brullé, *Batotheca* Enderlein, and *Conspinaria* Schulz) are associated with Limacodidae or Zygaenidae. Two genera of the *Rogas* group (*Megarhogas* and *Canalirogas*) are now known to be parasitoids of lymantriids, and the Afrotropical genus



Figures 18–28. Photographs of various Rogadini mummies with arrows indicating the emergence hole made by the adult parasitoid. (18) *Megarhogas* sp. ex *Perina nuda* (Fabricius) (Lymantriidae), India. (19) *Megarhogas* sp., India. (20) *Rectivena* sp., ex limacodid larva, Nigeria. (21) *Spinaria* sp., ex *Sitora nidens* Walker (Limacodidae), Java. (22) *Batotheca* sp., ex limacodid on *Adhatoda vasica* Nees (Acanthaceae) leaf, India. (23) *Hemigyroneuron* sp., ex unidentified species of Geometridae on toon leaf, India. (24) *Aleiodes lymantriae* Watanabe, ex. *Lymantria dispar* (L.) (Lymantriidae), Japan. (25) *Aleiodes* sp. ex *Remigia repanda* (Fabricius) (Noctuidae). (26) *Aleiodes narangae* (Rohwer) ex *Naranga aenescens* Moore (Noctuidae), on rice. (27) *Aleiodes* sp. ex *Trichoplusia ni* (Hubner) (Noctuidae), Thailand. (28) *Canalirogas* sp. aff. *balgooyi* ex unidentified 'nettle caterpillar' (=unidentified Lymantriidae) on clove, Sumatra.

Table I. Summary of host and mummy features of Rogadinae.

Genus	Figure	Host group	Degree of tanning/ hardening of mummy	Position of emergence hole (N=number of specimens seen by us)
Aleiodes	22, 24–26	Many host families but not Limacodidae	Very strong, hard, usually dark brown	Postero-dorsal (N>1000)
Hemigyroneuron	23	Lasiocampidae[a] and Geometridae	Very strong, hard, dark brown	Postero-dorsal (N=1)
Macrostomion	31	Sphingidae[b]	Moderate	Gregarious: various irregular positions (N=4)
Rogasodes	8	Drepanidae	Very weak	Postero-ventral (N=1)
Canalirogas	27	Lymantriidae	Moderate	Postero-dorsal (N=1)
Megarhogas	17, 18	Lymantriidae[c,d]	Very weak	Postero-lateral (N=2)
Pholichora		Geometridae[e]	Unknown	Unknown
Rogas	30	Limacodidae	Rather weak	Postero-dorsal (N=2)
Rectivena	19	Limacodidae[a]	Weak	Postero-dorsal/dorsolateral (N=2)
Darnilia		Limacodidae[f]		
Triraphis	28, 29	Limacodidae and Zygaenidae[a]	Rather weak	Postero-dorsal/dorsolateral (N=5)
Batotheca	21	Limacodidae[g]	Rather weak	Postero-dorsal/dorsolateral (N=2)
Spinaria	20	Limacodidae[g]	Rather weak	Postero-dorsal/dorsolateral (N=2)
Conspinaria		Zygaenidae[h]	Moderate but hosts with thick cuticle	Posterior; various orientations (N=3)
Yelicones		Pyralidae[i]	Moderate	Posterior and anterior, dorsal
Clinocentrus		Several host families (“Microlepidoptera”)	Usually moderate to strong	Anterior; various orientations (N>100)
Stiropius		Bucculatricidae and Lyonetiidae[j]	Very weak	Anterior; dorsal (N=6[k])

References to hosts: [a]van Achterberg (1991); [b]Shaw (2002); [c]Watanabe (1932); [d]Chen and He (1997); [e]Quicke and Shaw (2005); [f]van Achterberg (1989); [g]Austin (1987); [h]Quicke et al. (2003); [i]Quicke and Kruft (1995); [j]Whitfield (1988). [k]Five of these reported to us by J. B. Whitfield (personal communication).

Pholichora is apparently a parasitoid of Geometridae (Quicke and Shaw 2005). Until a more detailed phylogeny of the *Rogas* group is available it is not possible to be certain about which host group is ancestral, though it seems that Limacodidae and/or Zygaenidae may be on account of the broad spread of taxa associated with them.

Within the Rogadinae, the relationships of *Rogasodes* and *Rogasella* are hard to determine, because of both the lack of an adequate genus-level phylogenetic framework and their scarcity in collections, which means that no specimens have been available for dissection or for DNA sequencing. The long metasoma, strongly curved ovipositor and the presence of a comb on the hind tibia all suggest a relationship with the *Rogas* group of genera, though probably all of these characters are homoplastic. Further, van Achterberg and Chen (1996) note the considerable similarity between *Rogasella* and *Canalirogas*, and it is therefore likely that they belong to the same clade. In this case, Drepanidae can be added to the hosts known to be utilized by members of the *Rogas* group of genera.

Survey of mummy types and emergence of Rogadinae

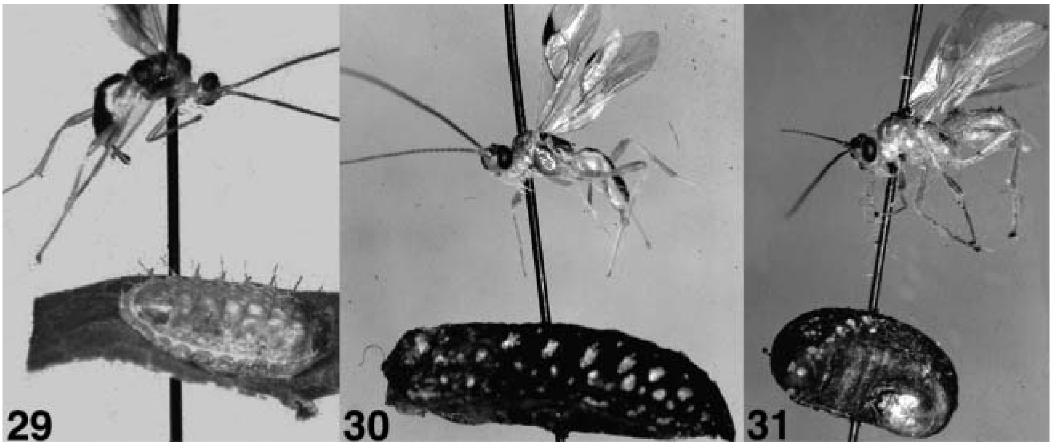
A particular characteristic of the Rogadinae is the mummification of the host larva, inside which the parasitoid pupates and from which the adult subsequently emerges. These are important stages in the parasitoid's life history, and undoubtedly will have been subjected to selection pressure: neither the structure of the mummy nor the way in which the adult emerges is uniform in the subfamily, and here we attempt to place the variation seen into a possible phylogenetic context. Information on the nature of the mummies produced by rogadine wasps and on the position of the adult's emergence hole is provided in Table I.

Molecular and morphological considerations place the Clinocentrini and Stiropiini as two of the most basal clades of the Rogadinae *sensu stricto* (Chen et al. 2003; Zaldivar-Riveron et al. 2004, forthcoming; Areekul et al. forthcoming), and almost certainly the Clinocentrini constitutes the sister group of the rest of the subfamily. The position of the Stiropiini is less clear and it is most likely either the sister group of the rest of the Rogadinae excluding the Clinocentrini, or the sister group of the *Rogas* group. These taxa may therefore be used to infer the plesiomorphic emergence condition. In both these tribes it is the cocooned prepupa that is mummified, there is no terminal contraction of segments, and the emergence hole from the mummy is always close to the head end of the host larva (Shaw 1983; Whitfield 1988). This is in strict contrast to the reliably posterior position seen in the Rogadini (except for the gregarious species of *Macrostomion*; see below and Figure 32). In the Clinocentrini (Figures 34, 35), the emergence hole is seemingly random in terms of its dorso-ventral positioning (M. R. Shaw, unpublished observations based on more than 100 mummies formed by collectively six species of *Clinocentrus* Haliday), while in the Stiropiini emergence is apparently always more or less dorsal (six mummies formed by collectively three species of *Stiropius* Cameron) (Figure 36). The difference seen in these two tribes may reflect the difference in the pupation behaviours of their hosts. In the cases of the *Clinocentrus* species seen, the host cocoon is either rudimentary or of a soft silken structure with no particular dorso-ventral differentiation, and there is no particularly easy escape route for the adult parasitoid. The hosts of *Stiropius* (including *Viridipyge* Whitfield) seen, however, make more robust and specialized cocoons and, given the cocoon structure of the hosts of *Stiropius* s. str. (*Bucculatrix* species (Bucculatricidae) whose cocoons are stuck down ventrally), it is easy to see that emergence from the dorsal aspect of the host mummy, which is always distal to the side of the cocoon that is stuck down, would provide the easiest escape route from the host cocoon.

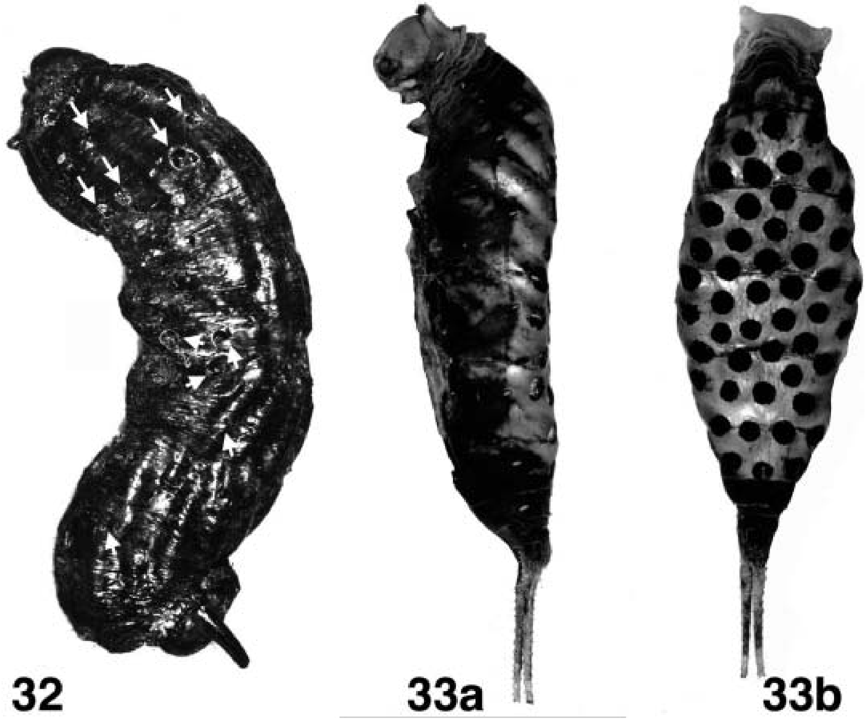
The relationships of the Yeliconini, comprising only the genus *Yelicones* Cameron, are less certain. They lack the conspicuously synapomorphic cone of filaments within the secondary venom duct that appear to constitute a synapomorphy for a group comprising *Aleiodes* and allies, and the *Rogas* and *Spinaria* groups (Zaldivar-Riveron et al. 2004). Unfortunately existing molecular data do not resolve its position convincingly, generally placing it (probably along with *Bulborogas* van Achterberg and *Pseudoyelicones* van Achterberg, Panteado-Dias and Quicke whose biologies are not yet known) between the *Aleiodes* group and the *Rogas* group but often unresolved even with respect to the Clinocentrini (Zaldivar-Riveron et al. forthcoming; Areekul et al. forthcoming; M. Mori et al., in preparation). Thus, the best estimate of the phylogeny of the Rogadinae based on a consensus of morphological and molecular data places *Yelicones* as just basal to the *Aleiodes* + *Rogas* group. We have seen one mummy each of two different *Yelicones* species, one (*Y. delicatus* Say) from North America and the other (*Y. koreanus* Papp) from India, both probably reared from Pyralidae (Figures 37, 38, respectively). The mummies bear a close resemblance to one another but differ in the orientation of the emergence hole. In both mummies the pupation chamber comprises the first five abdominal segments, is strongly lined with silk, and is isolated by a thick silk pad from the remaining body segments each side of it, which are curved ventrally, quite sharply so at the thoracic end.

The unused segments at each end are distended, rather than being strongly contracted (see below for further comment). In both cases the *Yelicones* mummies are regular in shape about a longitudinal axis, and therefore the curvature of both ends lies in the same plane, but the axis is not precisely dorsoventral with respect to the host's integument, with the result that all of the prolegs are more or less ventro-laterally positioned on one side. Emergence was strictly dorsal with respect to the shape of the mummy, in one case towards the host's head end (Figure 37) and in the other posteriorly (Figure 38). Emergence was clearly in the easiest position for escape, avoiding the down-curved, unoccupied parts of the mummy, but the limited sample of only two mummies indicates that orientation relative to the host end is not fixed. Importantly, these two mummies were certainly not attached to any substrate, and seem most likely to have been formed from prepupal hosts within cocoons (though evidence for this is lacking).

From Table I it is apparent that the familiar highly tanned and hard mummies of solitary *Aleiodes* species (Figures 24–27) are not typical of the Rogadini as a whole. The only other genus with a similarly hard, dark, and tanned mummy seen by us is *Hemigyroneuron* Baker (Figure 23) which, according to the venom apparatus study by Zaldivar-Riveron et al. (2004), also belongs to the *Aleiodes* group. In contrast, the mummies made by members of the *Rogas* group of genera are typically weakly sclerotized (e.g. Figures 8, 18–21, 29) or if apparently thicker and harder as in some Spinariina, and also *Triraphis* and *Rogas*, this is due to the skin of the host caterpillar's cuticle being much thicker and tougher as is often the case with late instar Limacodidae (e.g. Figures 22, 30, 31). Further, whereas *Aleiodes* species invariably emerge from the posterodorsal part of the mummy, many of the other genera regularly emerge dorso-laterally or laterally, as well as sometimes from a less extreme posterior position. Emergence of *Rogasodes* from the ventral surface of the mummified host is therefore consistent with its belonging to the *Rogas* group of genera. The degree of specialization in *Aleiodes* in comparison with the *Rogas* group is apparent even in gregarious species. Figure 32 shows the mummified remains of a sphingid host of a *Macrostomion* species (i.e. *Rogas* group), and it can be seen that the individual parasitoid cocoons within it are arranged longitudinally throughout most of the host's body, emergence occurring all around the circumference with both posterior and anterior



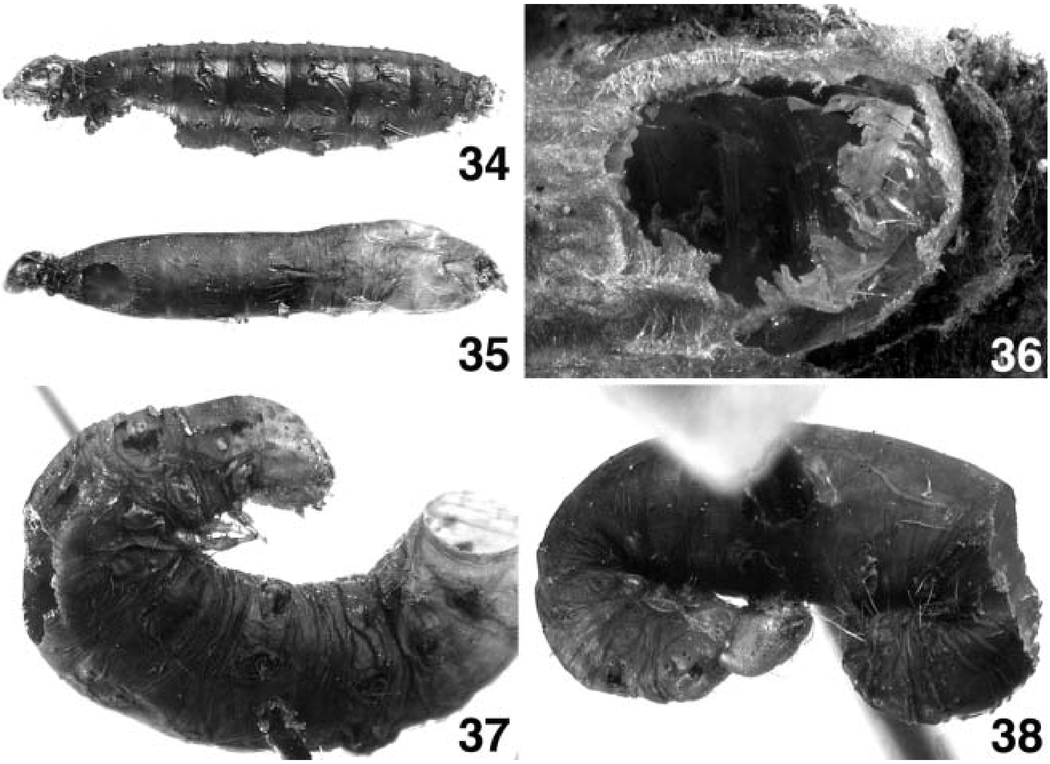
Figures 29–31. Photographs of various Rogadini mummies. (29) *Triraphis tricolor* (Wesmael), ex *Apoda limacodes* (Hufnagel) (Limacodidae). (30) *Triraphis tricolor*, ex *Apoda limacodes*, an instar later than in Figure 29. (31) *Rogas luteus* Nees ex *Apoda limacodes* (prepupal, extracted from cocoon).



Figures 32, 33. Photographs of gregarious Rogadini mummies. (32) *Macrostomion gnathothlibi* Shaw, ex *Gnathothlibus erotus eras* (Boisduval) (Sphingidae), with arrows indicating some of the emergence holes. (33) *Aleiodes pallescens* Hellén ex *Cerura vinula* (Linnaeus) (Notodontidae): (a) lateral and (b) dorsal aspects of mummy to show highly ordered alignment of individual *Aleiodes* pupation chambers.

emergence seen from the same mummy (Shaw 2002). In contrast, the gregarious *Aleiodes pallescens* Hellén, which attacks the notodontid *Cerura vinula* (L.), has its pupae all orientated obliquely dorsoventrally with the emergence holes being as dorsal as possible and as far posterior as possible (Figure 33).

In *Aleiodes* mummy structure varies considerably (Figures 24–27, 33, 39–42; see also Shaw et al. 1997, 1998a, 1998b; Marsh and Shaw 1998). The most basal clade of the species whose mummies we have been able to examine belong to the subgenus *Chelonorhogas* Enderlein (Zaldivar-Riveron et al. 2004; M. Mori et al., in preparation; our view that this clade is relatively basal, which is strongly supported by molecular evidence, is at varience with that of Fortier and Shaw 1999, Figure 3) and are characteristically relatively large parasitoids of Noctuidae, which they kill before the host is fully grown. In temperate areas these *Aleiodes* are typically univoltine species in which the mummy is used for diapause, and it may need to persist for up to 10 months before emergence. Typically these mummies are well-lined with silk and in many species they are strongly stuck down to a substrate such as a twig by fluids expelled through the venter of the strongly contracted thoracic region of the host (cf. Shaw et al. 1997, Figures 31, 32; 1998a, Figure 15). This configuration, like that of *Yelicones* mummies, may have strongly conserved a dorsal emergence position, allowing the easiest escape, but emergence would also have been facilitated by its caudal orientation, thereby fully removing the need for the emerging adult to chew through the most hardened and modified (anterior) part of the



Figures 34–38. Photographs of Clinocentrini, Stiropiini, and Yeliconini mummies. (34) *Clinocentrus cunctator* (Haliday), ex *Anthophila fabriciana* (Linnaeus) (Choreutidae), showing antero-ventral emergence. (35) *Clinocentrus hungaricus* Szépligeti, ex *Ypsolopha vittella* (Linnaeus) (Yponomeutidae). (36) *Stiropius bucculatricis* (Ashmead), ex *Bucculatrix*, partly exposed in situ in host cocoon showing ragged antero-dorsal emergence hole in the very thin transparent host mummy. (37) *Yelicones delicatus* Say ex *Psorosina hammondi* (Riley) (Pyralidae), showing antero-dorsal adult emergence hole at left. (38) *Yelicones koreanus* Papp, ex pyralid larva, postero-dorsal adult emergence hole.

Figure 39. *Aleiodes* sp., ex *Eupithecia assimilata* Doubleday (Geometridae): (a) lateral and (b) dorsal aspects.

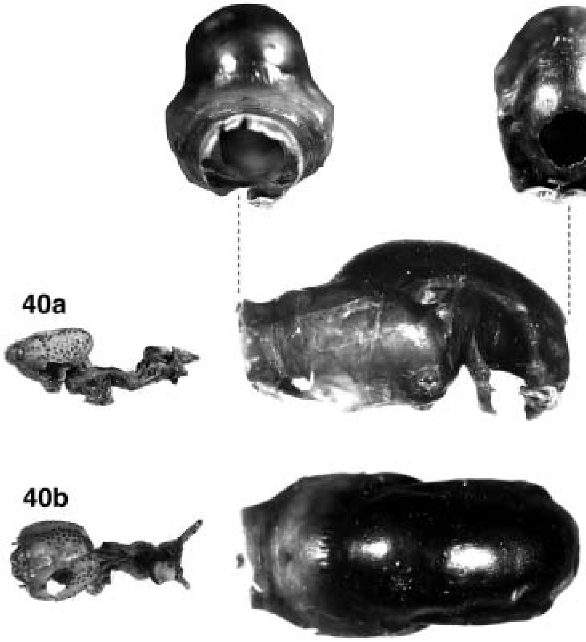


Figure 40. *Aleiodes albitibia* (Herrich-Schaeffer), ex *Notodonta dromedarius* (Linnaeus) (Notodontidae): (a) lateral and (b) dorsal aspects, with anterior and posterior views also indicated.

mummy. In other *Aleiodes* species, the mummy period often has a shorter duration, and the mummy is rather less tough. In some cases it is made within the host's cocoon-like retreats and may be scarcely or even not at all stuck down to the substrate. Even in these, fluids are always expelled through a ventral or more complete opening made towards the anterior end, but the posterodorsal emergence position has been strongly conserved. These features are apparent even in the gregarious *A. pallescens* (Figures 33, 34), as well as in species in

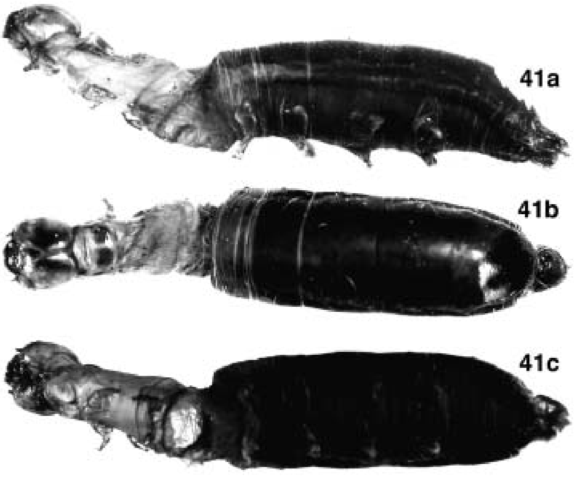


Figure 41. *Aleiodes unipunctator* (Thunberg), ex *Apamea unanimis* (Denis and Schiffermüller) (Noctuidae): (a) lateral, (b) dorsal and (c) ventral aspects, the latter showing the site of weak attachment as a hole.

Figure 42. *Aleiodes praetor* (Reinhard), ex *Lathoe populi* (Linnaeus) (Sphingidae): (a) lateral and (b) dorsal aspects.

which the mummy is either not stuck down (e.g. Figure 39, and also *A. pallidator* (Thunberg), *A. modestus* (Reinhard), *A. compressor* (Herrich-Schaeffer)) or, in the exceptional mummy of *A. albitibia*, not only not stuck down but also lacking the anterior part of the host (Figure 40). Thus in the Rogadini, the contrast between *Aleiodes* (and *Hemigyroneuron*) and those genera in which emergence is less consistently dorsal may largely reflect a different ancestral habit, as mummification in prepupal retreats occurs frequently in the *Rogas* group of genera whose mummies are, even when made in an exposed situation, neither as heavily tanned nor as strongly fixed down as seen in the apparently basal condition for the genus *Aleiodes*. Within the Rogadini the posterior emergence position seems to be general except that among gregarious species (of which rather few are known) only *Aleiodes* seems to have the strict behavioural organization for this to persist (contrast *Macrostomion*, Figure 32, with *A. pallescens*, Figure 33). Thus, in the Rogadini, the posterior emergence orientation appears to have arisen early, with strict dorsal positioning having its enduring origin in the strongly stuck down mummies that appear to be the basal condition within *Aleiodes*.

Finally, some observations on the pattern of occurrence of uncontracted parts of mummies within the Rogadinae are worth adding. In *Yelicones* (Yeliconini) both the mummies seen had uncontracted parts more or less curved down at each end of the central pupation chamber, and it seems likely that these would initially have been recepticals for excess fluid as the pupation chamber was being isolated. In the species of *Stiropius* (Stiropiini) that we have seen the pupation site appears to be more or less coextensive with the entire body of the prepupal host, and this is true also of some *Clinocentrus* (Clinocentrini) (Figure 34) in which fluid is definitely expelled through a slit towards the caudal end as the mummy forms (M. R. Shaw, personal observation). However, in some other *Clinocentrus* species (Figure 35) the caudal end remains as an uncontracted sac, isolated (as in *Yelicones*) by a silken partition from the pupation chamber. In *Aleiodes* (Rogadini) the usual form of the mummy involves a posterior pupation chamber with the anterior end of the host contracted (and usually, but not always, stuck down by expelled fluids), but in a few species the anterior end usually remains more or less distended (Figure 41) although the mummy is usually at least weakly stuck down. The remarkable and highly aberrant mummy of *Aleiodes albitibia* (Herrich-Schaeffer) (Figure 40) goes a stage further, in that the anterior part of the caterpillar detaches, initially filled with fluid, and the mummy made out of the posterior part (which has a swollen, empty space ventro-anterior to the pupation chamber) is not stuck down. The detachment of the anterior end of the host in the process of mummification is also a characteristic of the only distantly related *Aleiodes praetor* (Reinhard) (Figure 42; see also Shaw et al. 1988b, Figure 2), but in this case the detached structure is not particularly fluid-filled, there is no inflated void next to the pupation chamber, and the mummy is strongly stuck down.

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