RESEARCH ARTICLE

Emergence behaviour of adult *Trogus lapidator* (Fabricius) (Hymenoptera, Ichneumonidae, Ichneumoninae, Heresiarchini) from pupa of its host *Papilio machaon* L. (Lepidoptera, Papilionidae), with a comparative overview of emergence of Ichneumonidae from Lepidoptera pupae in Europe

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Abstract

Unusually for Ichneumonidae, *Trogus lapidator* emerges through a hole in the pupal wing case of its papilionid butterfly host that is made largely by a liquid secretion that softens and disintegrates the host tissue. The mandibles are deployed to help spread the secretion, but only towards the very end of the emergence process are they used (and then only in a minor way) to enlarge the hole. Links to video clips showing the emergence of *T. lapidator* are provided. Photographs illustrating the nature of emergence holes left in Lepidoptera pupae by a range of Ichneumonidae and some Chalcidoidea are presented and discussed, contrasting with the emergence hole left by *Trogus* and close allies.

Keywords

Pupal cuticle, eclosion, cuticular disintegration, staining, cap-cutting, mandibular structure

Introduction

One of the general functions of the mandibles of adult Hymenoptera is to aid emergence from the cocoon or other pupation site, although the wide range of variation of mandibular structure suggests that this is not always achieved in the same way, and indeed often indicates other functions for the mandibles too (undoubtedly including nest-building, prey manipulation, accessing hosts, and feeding; uses of the mandibles that are well-known in many relevant taxa). Many Ichneumonoidea pupate in well-defined cocoons, from which adults of various groups emerge by cutting a cap or strips with great precision, but others chew more or less irregular holes for the purpose. In contrast with Braconidae (the small subfamily Meteorideinae and a small and unusual subtribe, Aspidobraconina, of Braconinae aside), many Ichneumonidae emerge as adults from Lepidoptera pupae, whether as true pupal parasitoids (some Pimplinae, many Ichneumoninae, a few Cryptinae), or as larva-pupal parasitoids (Metopiinae, most Anomaloninae, many Ichneumoninae, occasional Campopleginae). In these cases it is usual for adult emergence to be either through a roughly shaped chewed hole, typically subapical, around which a scattering of bits of host cuticle can be found, or in many cases though the hole left by a more neatly cut and more or less detached apical cap (sometimes partly assisted by the host's dorsal ecdysal sutures).

Trogus lapidator (Fabricius) is a widespread specialist koinobiont parasitoid of the Swallowtail Butterfly *Papilio machaon* Linnaeus (Papilionidae) in Europe, with rare confirmed records from the more restricted *Papilio alexanor* Esper (e.g. Sanetra 1998). The European nominal taxon *Trogus violaceus* (Mocsáry), which is confined to Corsica and Sardinia where it parasitizes both *P. machaon* and *P. hospiton* Guenée, is regarded as a synonym of *T. lapidator* by Wahl and Sime (2006). *Trogus* is a genus of about twelve species (Wahl and Sime 2006) of larva-pupal parasitoids of *Papilio* occurring in the Palaearctic and New World, and all probably have similar biology, invariably emerging as adults through the wing case of the host pupa. Closely related taxa such as *Psilomastax pyramidalis* Tischbein, parasitizing *Apatura* spp. (Nymphalidae: Apaturinae) make similar emergence holes, presumably in the same way, though in the case of *Psilomastax* the emergence hole is substantially more ventral. According to Sime and Wahl (2002) in their cladistic analysis of the *Callajoppa* genus-group, emergence through the wing case (their character 58) is unique to the *Trogus*-subgroup, which contains several additional genera.

During filming of the life history of *Papilio machaon* and its parasitoids by the second and third authors (included in https://youtu.be/PsU5rqeIXBg?list=PLLIrjN9bA2GwtZiIlVdmHwOcTUzk6q-6V, https://youtu.be/4K6F_pr1Om4?list=PLLIrjN9bA2GyWrineNq9vnKCct17m1ewH, https://youtu.be/GdBKDTYR57o?list=PLLIrjN9bA2GzkK_g-Tbq9odQYgt_mX1BS, https://youtu.be/6qygQ62nQWQ?list=PLLIrjN9bA2GxY-BAR-nHRUfcADsXSRytF, and https://youtu.be/fchB-w67vTg?list=PLLIrjN9bA2Gwd7MyVv2im_Sbq-jly4Kl_) as part of their project to

document the natural history of the French department of Var, the remarkable sequences showing the emergence of adult *Trogus lapidator* (https://www.youtube.com/watch?v=GrhKhsj00BE and https://www.youtube.com/watch?v=y_p8QcnHgjs) presented and discussed in this paper were brought to the attention of the first author. In order to set this in context, a brief illustrated overview of emergence from pupae of Lepidoptera by Ichneumonidae is given. When possible we have paid particular attention to those parasitizing butterflies which, by often being relatively exposed (and sometimes needing to persist for much of the year), may be expected to sometimes have relatively hard thick cuticle similar to that of *P. machaon*. Several groups of Chalcidoidea also emerge as adults from the pupae of Lepidoptera, and very brief mention is made of some of these.

Materials and methods

Observations on *Trogus lapidator*, which has up to three annual generations in the region, were made and filmed during spring and summer 2013 in a large garden (1.5 hectares) in southern France (Var: Callas), where natural populations of the swallowtail butterfly *Papilio machaon* and various of its parasitoids, including *T. lapidator*, occurred. In some cases ovipositions by captive *T. lapidator* into middle instar host larvae had been witnessed and, following their pupation a week later and after the unwitnessed emergence of an adult *T. lapidator* several weeks later from a different pupa, two hosts were watched carefully for signs of adult emergence. The emergence process took place in late morning over a period of about 45 minutes and both cases were filmed with a Canon XL2 with a 20× L IS zoomobjectif XL 5.4-108mm with extender 72mm close-up lens 500D. The footage is registered on mini DV60 tapes. From the footage videos were made that can be seen at https://www.youtube.com/watch?v=GrhKhsj00BE and https://www.youtube.com/watch?v=y_p8QcnHgjs. Stills taken from these and another video resulting from a similar process were used for Figs 1–4 and 85.

The National Museums of Scotland (NMS) houses a large collection of western Palaearctic Ichneumonoidea, made special by the quantity of reared material it contains, particularly in respect of parasitoids of Lepidoptera. A survey of emergence patterns of adults from Lepidoptera pupae seen in the three main subfamilies of Ichneumonidae with this habit (Ichneumoninae, Anomaloninae and Metopiinae) as well as lesser groups (Pimplinae: Pimplini, and the few relevant taxa of Campopleginae and Cryptinae) was undertaken from this resource, with particular attention to emergence from butterfly hosts. We illustrate a particularly large number involving Ichneumoninae, as this subfamily has proved to be the most variable. The survey was briefly extended to Chalcididae and Pteromalidae. Digital photographs of host Lepidoptera pupal remains from which Ichneumonidae (or Chalcidoidea) had emerged were taken using a Nikon D80 with Medical Nikkor 120mm lens attachment.

Results

Trogus lapidator and close relatives

From the two sequences of the emergence of *T. lapidator* adults that were filmed (https://www.youtube.com/watch?v=GrhKhsj00BE and https://www.youtube.com/watch?v=y_p8QcnHgjs) it is clear that the emergence hole is made by a softening and dissociation of the host cuticle involving a wet process, presumably originating from a secretion (Figs 1–4). In the videos the mandibles can be seen partially protruding at various stages but, except possibly at the very end when their slight involvement in enlarging the hole is arguable, their role appears not to be to bite or chew, but rather to help spread fluid externally round the edge of the hole being created. The pupal remains of *P. machaon* from which *T. lapidator* has emerged, when they have dried, generally leave a clear sign of this process, both by the rim of the emergence hole having an almost molten appearance and by considerable staining (Figs 5–7). The pupal remains of *Apatura* spp. (Nymphalidae) from which the related *Psilomastax pyramidalis* have emerged typically show similar staining (Figs 8, 9).

Other groups of Ichneumonidae and Chalcidoidea that predominantly emerge from Lepidoptera pupae

Ichneumoninae

All Ichneumoninae are parasitoids of Lepidoptera, and virtually all emerge as adults from the host pupa (*Colpognathus* is an exception: Shaw and Bennett 2001). Some taxa oviposit into the host in its larval stage, and are clear koinobionts, while others attack pupae or prepupae and are essentially idiobionts.

The most obvious group to survey for signs of similar modes of emergence is the tribe Heresiarchini, to which the *Trogus*-subgroup belongs. In all examined taxa (species of *Amblyjoppa*, *Callajoppa*, *Coelichneumon* and *Syspasis*) of this tribe, other than the *Trogus*-subgroup, emergence has been by cutting a more or less neat cap from the anterior (capital) end of the host pupa (Figs 10–12), hereafter termed "type 1" emergence. There appears to be no sign of cuticular degradation or deformation, but slight staining is evident very narrowly around the extreme edge of the cut in the paler-coloured pupae (Fig. 10).

In the very large tribe Ichneumonini a surprising range of emergence patterns is seen. *Hoplismenus*, which are parasitoids of butterflies, appear always to display type 1 emergence, with sharp caps (Figs 13–16), and often (Figs 13–15) but not always (Fig. 16) there is clear staining at the margins of the cut. In certain other genera (e.g. *Virgichneumon* (Figs 32, 33)) cap-cutting also seems to be the rule, although sampling within and between genera is not extensive. On the other hand, in *Ichneumon* both type 1 cap-cutting (Figs 17–23) and subapical ventrally chewed holes (Figs 24–27), hereafter "type 2" emergence, are seen,
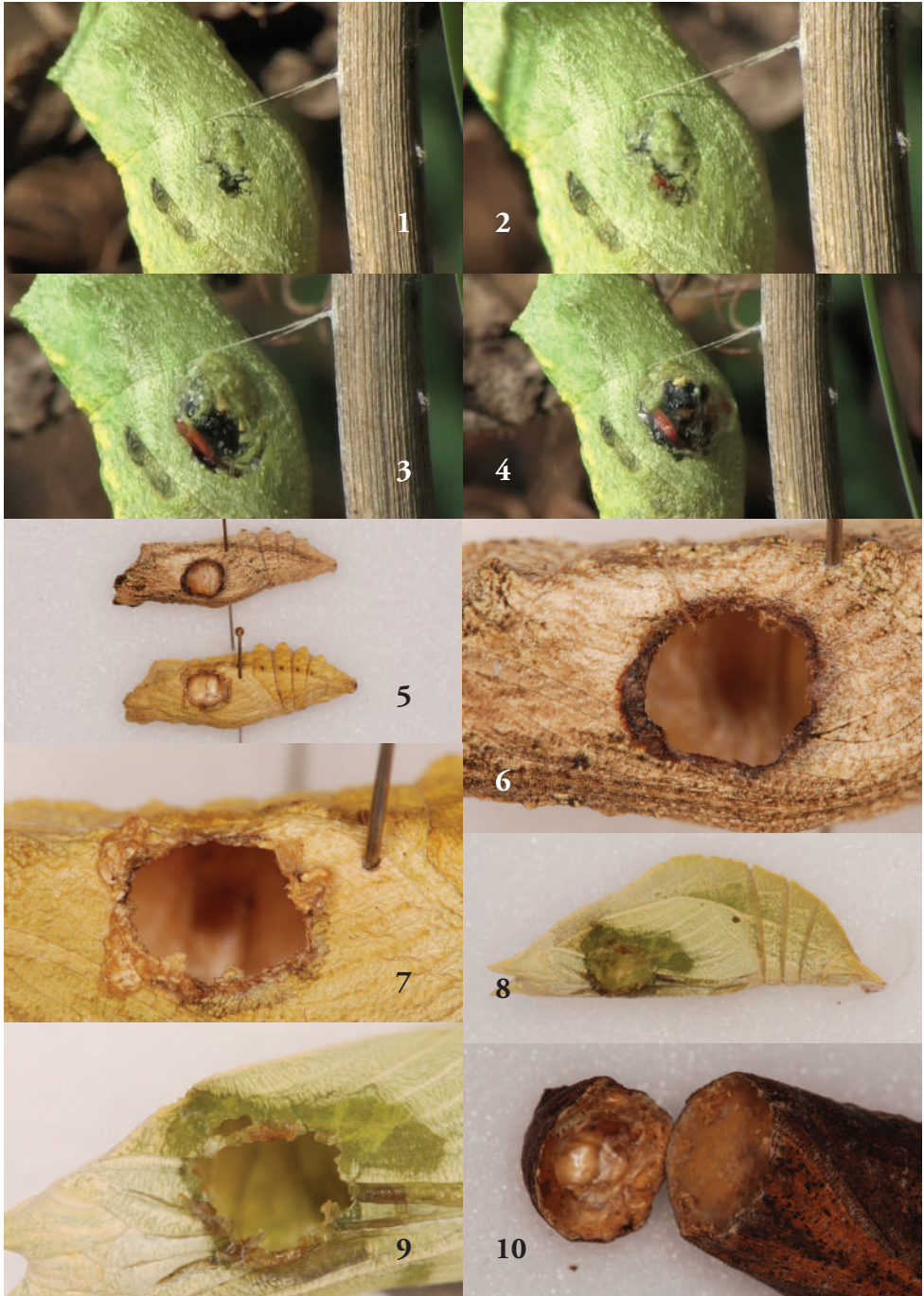
Figure 1–10. 1–4 Sequence in the emergence process of *Trogus lapidator* (Fabricius) from *Papilio machaon* Linnaeus (Papilionidae). **5–10** Host pupa following emergence of parasitoid. **5–7** *Trogus lapidator* from *Papilio machaon* **8, 9** *Psilomastax pyramidalis* Tischbein from *Apatura iris* (Linnaeus) (Nymphalidae) **10** *Amblyjoppa proteus* (Christ) from *Deilephila elpenor* (Linnaeus) (Sphingidae).
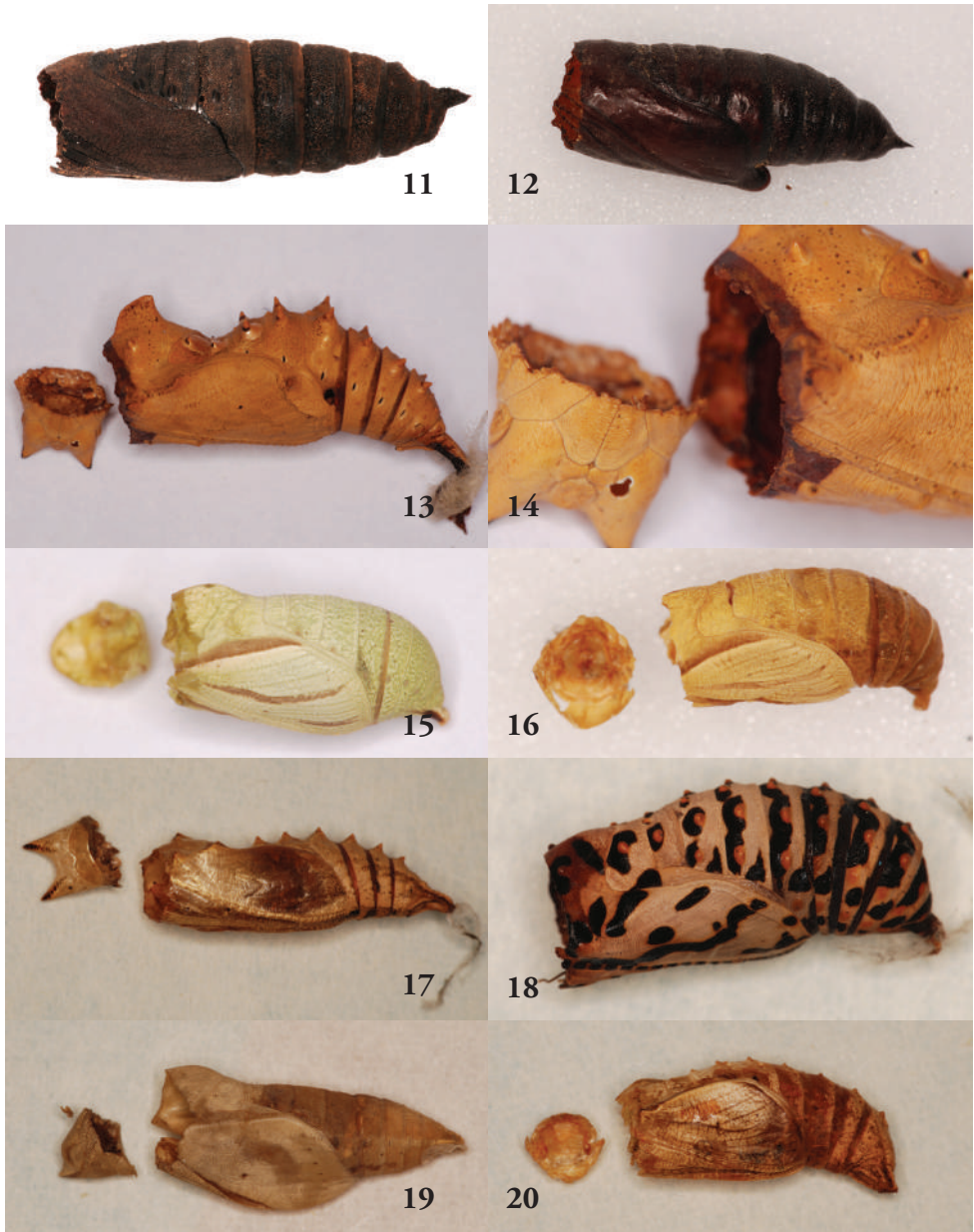
Figure 11–20. 11 *Callajoppa cirrogaster* (Schrank) from *Mimas tiliae* (Linnaeus) (Sphingidae) **12** *Coelichneumon litoralis* Horstmann from *Conisania andalusica* (Staudinger) (Noctuidae) **13, 14** *Hoplismenus terrificus* Wesmael from *Nymphalis polychloros* (Linnaeus) (Nymphalidae) **15, 16** *Hoplismenus bispinatorius* (Thunberg) from *Coenonympha pamphilus* (Linnaeus) (Nymphalidae: Satyrinae) **17** *Ichneumon cessator* Müller from *Aglais urticae* (Linnaeus) (Nymphalidae) **18** *Ichneumon stenocerus* Thomson from *Euphydryas aurinia* (Rottemburg) (Nymphalidae) **19** *Ichneumon quadrialbatus* Gravenhorst from *Colias croceus* (Geoffroy) (Pieridae) **20** *Ichneumon gracilicornis* Gravenhorst from *Boloria eunomia* (Esper) (Nymphalidae)

even within the species parasitizing butterflies. Usually, a given *Ichneumon* species is more or less consistent in habit (Figs 20–23; 24–26), though in some cases it seems clear that the origin of cap-cutting can be traced to eclosing through ventrally chewed slits, which may extend to detaching a cap (Figs 28, 29); i.e. there is a continuum between types 1 and 2. Both in *Ichneumon* (Figs 28, 29) and elsewhere in the tribe (*Amblyteles armatorius* Forster: Figs 30, 31) the two modes can sometimes be seen in the same species in different hosts, although there is insufficient evidence to decide whether this is genuinely host-related. Occasionally the process of detachment of an untidy (or small) cap may be aided by dorsal sutures in the host cuticle (Fig. 26), but this is by no means always the case and usually if a cap is detached it is chewed all round, even if untidily (Fig. 31). In the tribe as a whole cap-cutting ranges from very neat and complete (Figs 32–34) to haphazard (Fig. 31), and in many cases emergence through ventrally chewed holes does not lead to the detachment of a cap (e.g. Fig. 35). In uncommon situations, such as species parasitizing stem-inhabiting noctuids, the apical part of the pupa may be chewed away untidily (Figs 36, 37). Overall, the degree of staining seems rather inconsistent, though sometimes profound.

All members of the tribe Listrodromini parasitize lycaenid butterflies, and appear always to cut rather neat caps (type 1 emergence), seldom with much sign of staining (Figs 38–40).

Phaeogenini are all parasitoids of so-called microlepidoptera and, with the exception of the koinobiont *Epitomus* (Diller and Shaw 2014), they are essentially idiobionts. *Colpognathus* is exceptional in emerging from the mummified host larva (Shaw and Bennett 2001), but phaeogenines generally emerge from host pupae by chewing untidy subapical and more or less ventral holes. Any detachment of part of the pupa is incidental and usually ventro-apical, scarcely involving the dorsal part of the pupa, rather than fully apical (Figs 41–43), hereafter "type 3" emergence and regarded as relatively unspecialised, possibly reflecting the basal position of the tribe. However, in *Heterischnus* a facial cap is consistently and rather uniformly detached (Fig. 43). Staining is not usually evident.

In the koinobiont Platylabini, which all parasitize Geometridae or Drepanidae, rather variable cap-cutting (Figs 44-48) seems to predominate, though the origin as a ventral opening is sometimes clear when the cap has not been chewed all round and has failed to detach (Figs 49, 50), and sometimes the chewed hole is very untidy (Fig. 51). This is similar to the continuum between types 1 and 2 seen in Ichneumonini. A remarkable exception to the usual ventral position of emergence occurs in *Cyclolabus axillatorius* (Thunberg) (Figs 52, 53), in which all 3 examples seen have emerged through subdorsally chewed holes, with neither ventral damage to the host pupa nor detachment of a cap (other *Cyclolabus* species seen were unremarkable). Staining of the host pupal cuticle is generally absent.

Regarding the examined species in the small tribes, in Eurylabini an apical cap is sharply cut (Fig. 54), while in Goedartiini the adult emerges through a hole chewed in the apex of the pupa (Fig. 55). In Zimmerini the host pupal case of *Cotiheresiarches dirus* (Wesmael) is relatively frail and enclosed in a tough cocoon, and the problem of emerging from the latter causes the adult ichneumonid to leave the host pupa in a very damaged state, apparently a result of untidy and predominantly ventral tearing (Fig. 56).
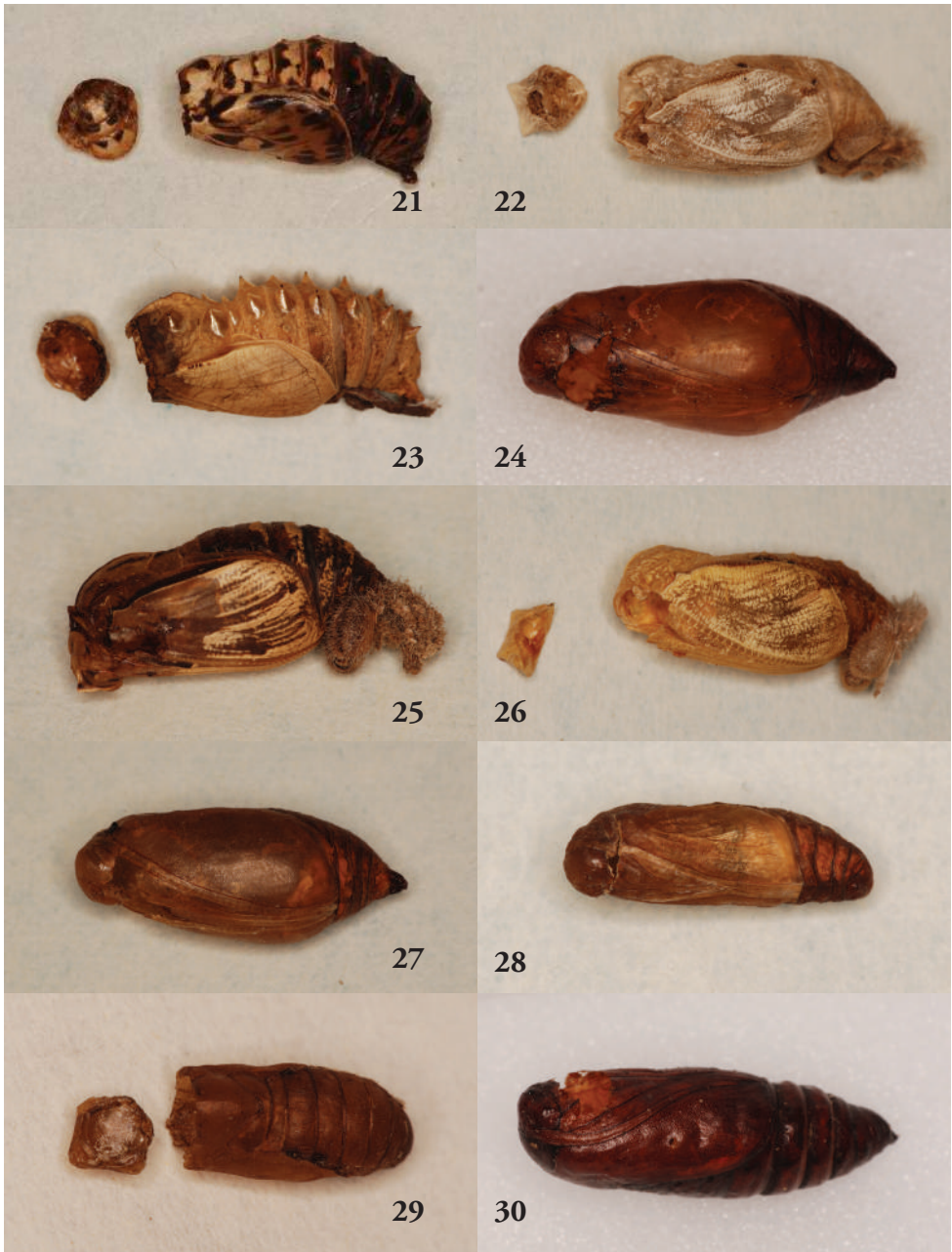
Figure 21–30. 21–23 Ichneumon gracilicornis from **21** *Melitaea athalia* (Rottemburg) (Nymphalidae) **22** *Maniola jurtina* (Linnaeus) (Nymphalidae: Satyrinae) **23** *Brenthis ino* (Rottemburg) (Nymphalidae) **24–26** *Ichneumon caloscelis* Wesmael from **24** *Hipparchia semele* (Linnaeus) (Nymphalidae: Satyrinae) **25** *Pyronia tithonus* (Linnaeus) (Nymphalidae: Satyrinae) **26** *Maniola jurtina* (Linnaeus) (Nymphalidae: Satyrinae) **27** *Ichneumon novemalbatus* Kriechbaumer from *Melanargia lachesis* (Hübner) (Nymphalidae: Satyrinae) **28, 29** *Ichneumon* cf. *exilicornis* Wesmael from *Agrodiaetus* sp. (Lycaenidae) **30** *Amblyteles armatorius* (Forster) from ?*Noctua* sp. (Noctuidae)
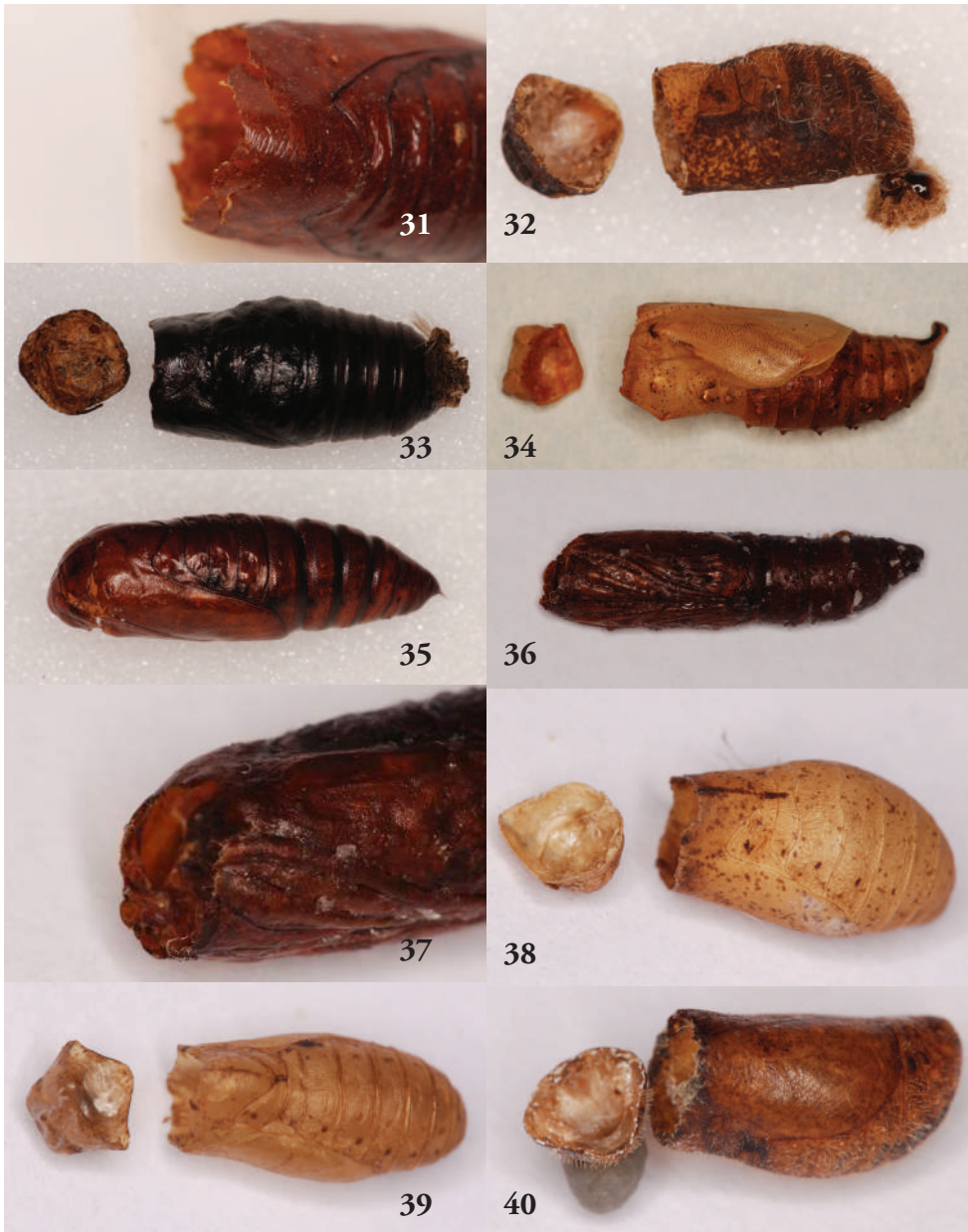
Figure 31–40.31 *Amblyteles armatorius* from ?*Xestia* sp. (Noctuidae) **32** *Virgichneumon tergenus* (Gravenhorst) from *Satyrium w-album* (Knoch) (Lycaenidae) **33** *Virgichneumon albilineatus* (Gravenhorst) from *Spilosoma* sp. (Erebidae: Arctiinae) **34** *Thyrateles camelinus* (Wesmael) from *Vanessa cardui* (Linnaeus) (Nymphalidae) **35** *Diphyus palliatorius* (Gravenhorst) from *Diarsia* sp. (Noctuidae) **36, 37** *Chasmias paludator* (Desvignes) from *Nonagria typhae* (Thunberg) (Noctuidae) **38** *Anisobas seyrigi* Heinrich from *Glaucopsyche melanops* (Boisduval) (Lycaenidae) **39** *Neotypus intermedius* Mocsáry from *Lampides boeticus* (Linnaeus) (Lycaenidae) **40** *Listrodromus nycthemerus* (Gravenhorst) from *Celastrina argiolus* (Linnaeus) (Lycaenidae).

Figure 41–50. 41 *Diadromus heteroneurus* Holmgren from *Ypsolopha vittella* (Linnaeus) (Ypsolophidae) **42** *Herpestomus brunnicornis* (Gravenhorst) from *Yponomeuta padella* (Linnaeus) (Yponomeutidae) **43** *Heterischnus truncator* (Fabricius) from indet. Pterophoridae **44** *Hypomecus quadriannulatus* (Gravenhorst) from *Cyclophora albipunctata* (Hufnagel) (Geometridae) **45** *Linycus exhortator* (Fabricius) from *Xanthorhoe fluctuata* (Linnaeus) (Geometridae) **46** *Platylabus dolerosus* (Gravenhorst) from *Chloroclysta* sp. (Geometridae) **47** *Platylabus vibratorius* (Thunberg) from *Eulithis testata* (Linnaeus) (Geometridae) **48** *Platylabus rufus* Wesmael from *Hydriomena furcata* (Thunberg) (Geometridae) **49** *Platylabus curtorius* (Thunberg) from *Phibalapteryx virgata* (Hufnagel) (Geometridae) **50** *Pristicerops infractorius* (Linnaeus) from *Cabera* sp. (Geometridae).

Anomaloninae

In this koinobiont subfamily the hosts are always attacked as larvae but emergence is invariably from the host pupa.

All data presented here pertain to the tribe Gravenhorstiini, which is exclusively associated with Lepidoptera. Examined taxa of *Aphanistes*, *Heteropelma*, *Therion* and *Trichomma* make detached caps, though not very neatly (Fig. 57) from their relatively large hosts, mostly having fairly tough pupae. In *Barylypa*, *Clypeocampulum* and *Erigorgus* type 2 emergence seems the rule (Figs 58–60), though in the case of *Clypeocampulum* the hole is not always ventral even in the same species (Figs 59, 60). Within *Agrypon* and *Habronyx* (*Camposcopus*) emergence is in most cases type 2 (Fig. 61) but in the former an irregular cap sometimes develops, although probably more by force than by cutting (Figs 62, 63), and only in relatively frail short-lived pupae. In one species (*Agrypon polyxenae* Szépligeti: Figs 61, 64) the position of emergence through a chewed hole is very consistently dorsal in one host genus (*Zerynthia* (Fig. 64), identical in all 29 examples from these slender hosts) but variable in another (*Archon*, one ventral (Fig. 61) and one dorsal in the two available examples from this differently shaped host). In the subfamily as a whole, appreciable staining is only rarely seen (e.g. Fig. 59).

Metopiinae

Notwithstanding some uncertainly placed taxa of unknown biology, all metopiines are believed to be koinobiont larva-pupal parasitoids of Lepidoptera.

In the genera *Chorinaeus*, *Hypsicera* and *Triclistus*, which mostly parasitize "microlepidoptera" with relatively frail (most often cocooned) pupae, emergence is generally type 2, through a chewed ventral hole (Fig. 65, 66), sometimes leading to the detachment of a rough-edged cap (Fig. 67); in *Scolomus* and *Synosis*, however, type 1 behaviour seems to be more common or possibly the norm (Figs 68, 69). In *Metopius* a very neat detached cap (type 1) is seen in taxa of the subgenus *Tylopius*, parasitizing weakly concealed tough pupae (Fig. 71), but species in the subgenus *Peltocharus* emerging from strongly cocooned hosts having less tough pupae chew a large ventral hole (Fig. 70).

Pimplinae: Pimplini

As a subfamily Pimplinae has very wide host associations and a correspondingly wide range of biology overall, but in the tribe Pimplini there are specialist idiobiont parasitoids of Lepidoptera pupae.

In the genera *Apechthis* and *Pimpla*, emergence is always through a chewed hole, usually rather irregular but with varying degrees of tidiness (Figs 72–75). Emergence is generally subapical but there is little consistency in position otherwise and ventral
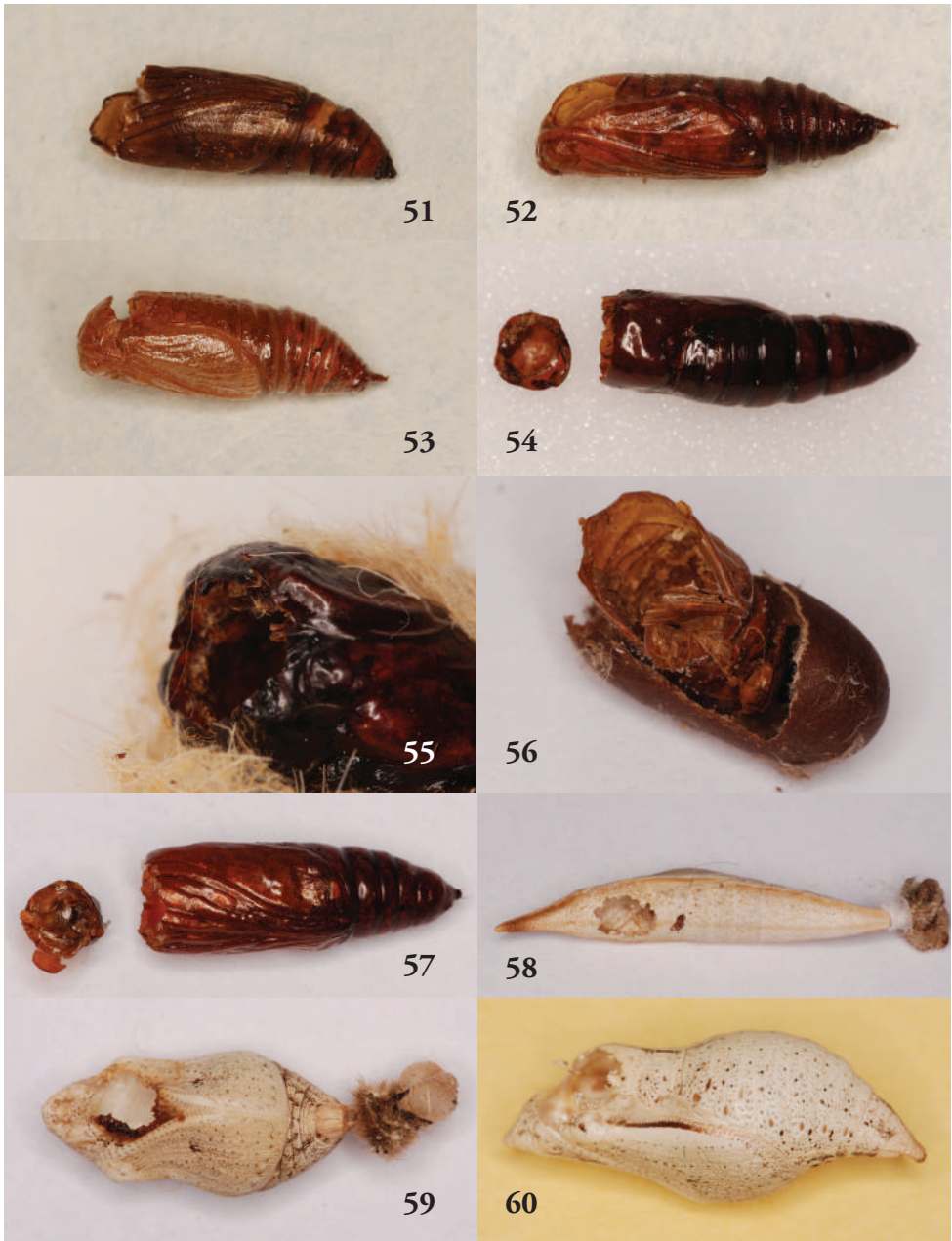
Figure 51–60. 51 *Apaeleticus bellicosus* Wesmael from *Idaea ochrata* (Scopoli) **52, 53** *Cyclolabus pactor* (Wesmael) from **52** *Eupithecia pimpinellata* (Hübner) (Geometridae) **53** indet. Geometridae **54** *Eurylabus torvus* Wesmael from *Eremobia ochroleuca* (Dennis & Schiffermüller) (Noctuidae) **55** *Goedartia alboguttata* (Gravenhorst) from *Calliteara pudibunda* (Linnaeus) (Erebidae: Lymantriinae) **56** *Cotiheresiarches dirus* (Wesmael) from *Eriogaster lanestris* (Linnaeus) (Lasiocampidae) **57** *Aphanistes gliscens* (Hartig) from *Dryobota labecula* (Esper) (Noctuidae) **58** *Clypeocampulum barbarae* Schnee from *Anthocharis euphenoides* Staudinger (Pieridae) **59, 60** *Clypeocampulum lubricum* (Atanasov) from *Zegris eupheme* (Esper) (Pieridae).
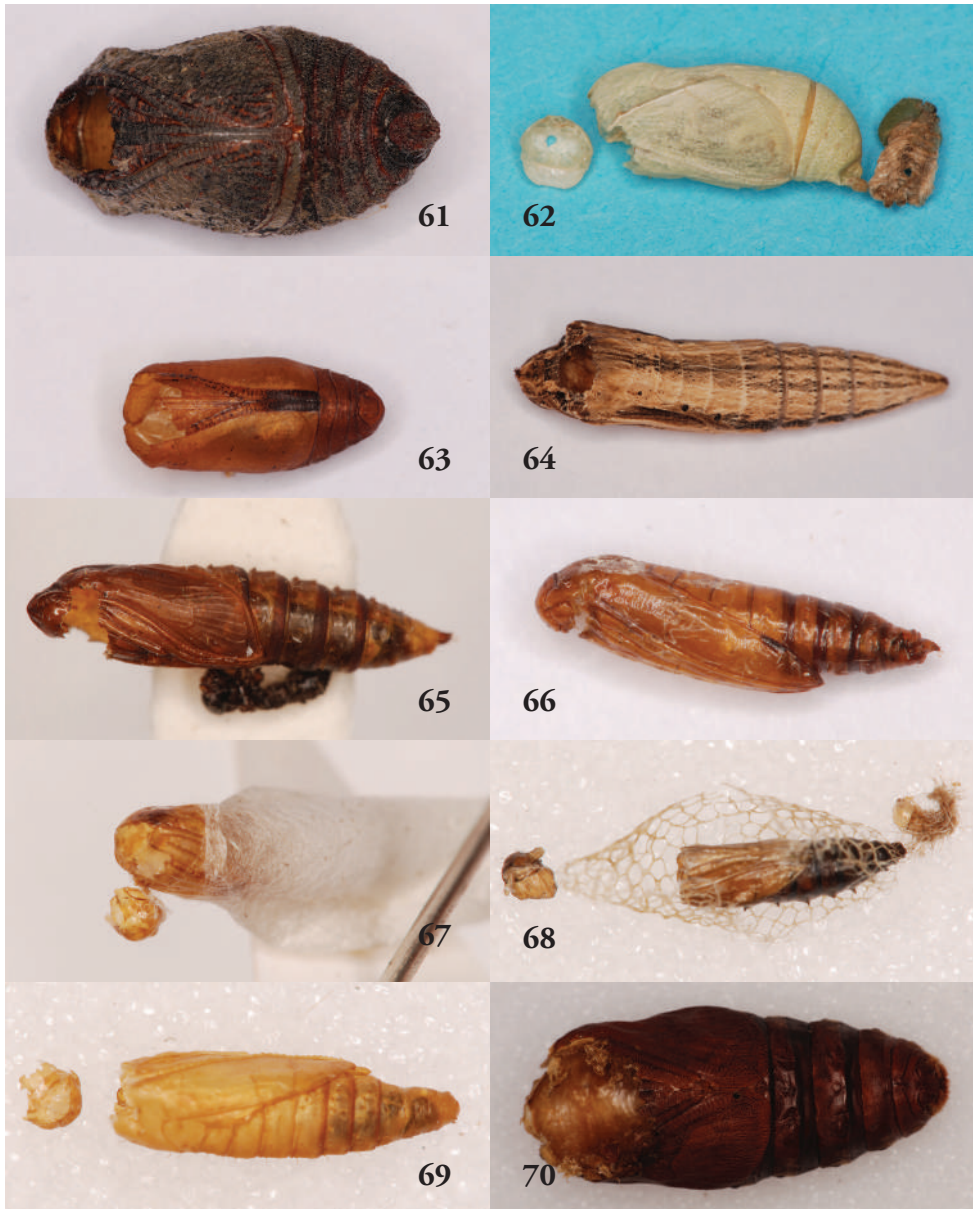
Figure 61–70. 61 *Agrypon polyxenae* (Szépligeti) from *Archon apollinus* (Herbst) (Papilionidae) **62** *Agrypon delarvatum* (Gravenhorst) from *Coenonympha* sp. (Nymphalidae: Satyrinae) **63** *Agrypon anomelas* (Gravenhorst) from *Agrodaetus* sp. (Lycaenidae) **64** *Agrypon polyxenae* from *Zerynthia polyxena* (Dennis & Schiffermüller) (Papilionidae) **65** *Chorinaeus funebris* (Gravenhorst) from *Clepsis spectrana* (Treitschke) (Tortricidae) **66** *Triclistus epermeniae* Shaw & Aeschlimann from *Epermenia chaerophyllella* (Goeze) (Epermeniidae) **67** *Triclistus anthophilae* Aeschlimann from *Anthophila fabriciana* (Linnaeus) (Choreutidae) **68** *Scolomus borealis* (Townes) from *Schreckensteinia festaliella* (Hübner) (Schreckensteiniidae) **69** *Synosis parenthesellae* Broad & Shaw from *Ypsolopha parenthesella* (Linnaeus) (Ypsolophidae) **70** *Metopius dentatus* (Fabricius) from *Lasiocampa quercus* (Linnaeus) (Lasiocampidae).
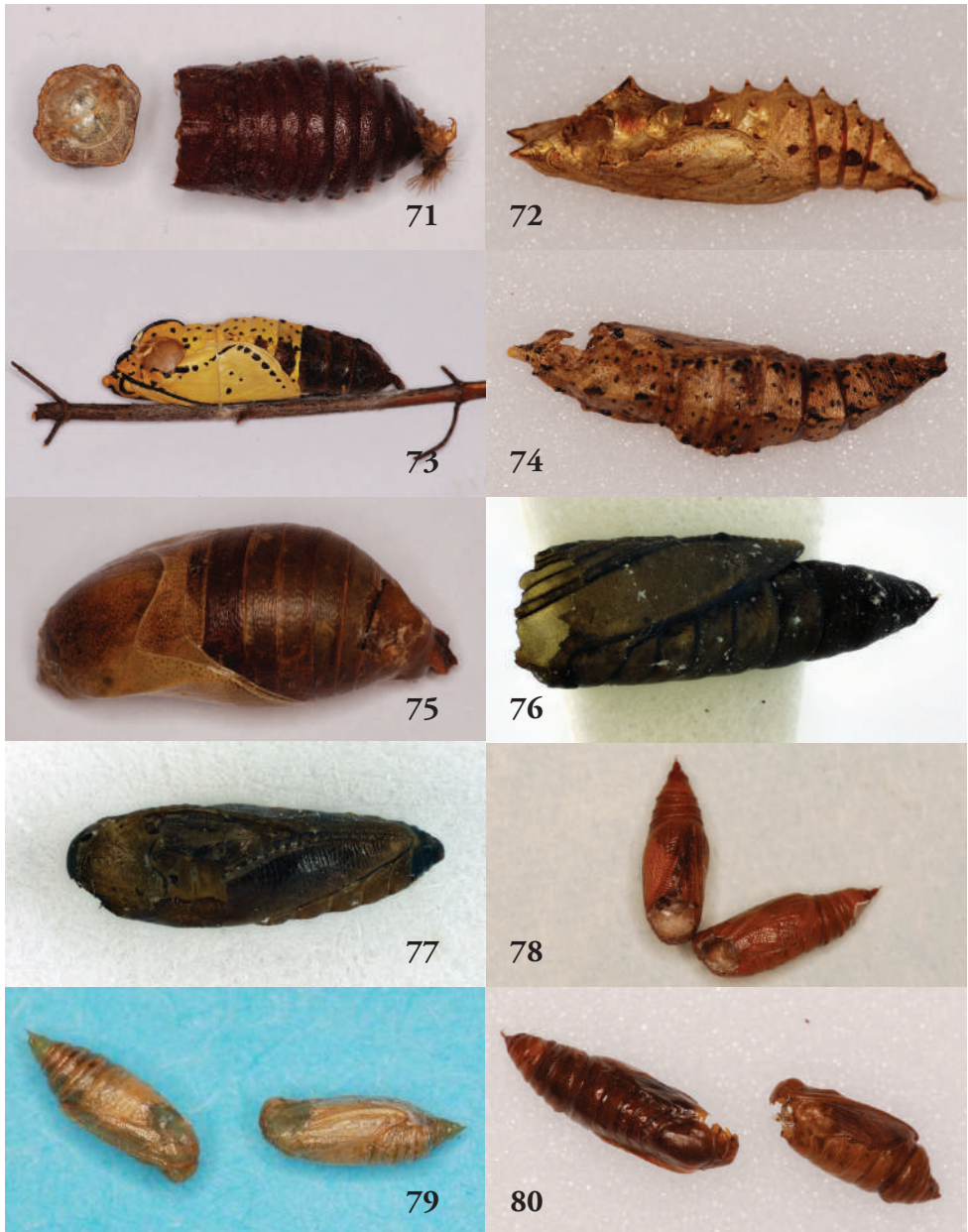
Figure 71–80. 71 *Metopius leiopygus* Foerster from indet. Arctiinae (Erebidae) **72, 73** *Apechthis compunctor* (Linnaeus) from **72** *Aglais urticae* (Linnaeus) (Nymphalidae) **73** *Aporia crataegi* (Linnaeus) (Pieridae) **74, 75** *Pimpla rufipes* (Miller) from **74** *Pieris brassicae* (Linnaeus) (Pieridae) **75** *Charaxes jassius* (Linnaeus) (Nymphalidae) **76** *Zoophthorus bridgmani* (Schmiedeknecht) from ?*Argyresthia* sp. (Argyresthiidae) **77** *Zoophthorus palpator* (Müller) from *Stephensia brunnichella* (Linnaeus) (Elachistidae) **78** *Campoplex brevicornis* (Szépligeti) from *Eupithecia venosata* (Fabricius) (Geometridae) **79** *Diadegma scotiae* (Bridgman) from *Phaulernis fulviguttella* (Zeller) (Epermeniidae) **80** *Dusona leptogaster* (Holmgren) from (left) indet. Geometridae and (right) *Alsophila aescularia* (Dennis & Schiffermüller) (Geometridae).

emergence is certainly not especially favoured. Rarely emergence towards the caudal end of the host pupa occurs (Fig. 75). Slight staining is sometimes seen (Fig. 73), and the arguably most specialised genus *Apechthis* often leaves clear signs of strip-cutting around its neater holes (Figs 72, 73).

Cryptinae

As a subfamily Cryptinae has a very wide host range, in which Lepidoptera do not play a dominant part. A few of the idiobiont species directly associated with Lepidoptera in Europe, however, do emerge as adults from the host pupa, and in some genera this may be normal.

The only relevant genus for which we have seen host remains is *Zoophthorus* (Phygadeuontini) (Figs 76, 77), in which unspecialised type 2 or type 3 emergence is found, similar to that in Phaeogenini.

Campopleginae

A large part of this koinobiont subfamily is associated with Lepidoptera but almost all kill and erupt from the host before it pupates. In some genera species that occasionally kill the host after its pupation are found but it is not usually a consistent strategy and, in general, if pupation takes place within the host pupa it is ruptured during the process of cocoon construction by the parasitoid, as occurs also in a few species of *Ophion* (Ophioninae).

However, odd species in genera such as *Campoplex* (Fig. 78), *Diadegma* (Fig. 79) and *Dusona* (Fig. 80, 81) consistently pupate within the unruptured pupal shell of their hosts, although sometimes within at least a frail cocoon of their own as well (Fig. 78). In all these cases the emergence hole is generally of the least specialised kind (albeit that emergence is generally at the head end), through a subapical chewed hole lacking consistent dorso-ventral orientation and with no tendency for detachment of a cap. Staining is not evident.

Chalcidoidea

Several families of Chalcidoidea include idiobiont parasitoids that attack and emerge as adults from Lepidoptera pupae.

In *Brachymeria* (Chalcididae) emergence is through a chewed hole, usually in a subapical position (Fig. 82) or more or less laterally (Fig. 83), but with little evident orientation otherwise. Often there is considerable staining (Fig. 83).

A few species of *Pteromalus* (Pteromalidae) and some related genera that attack Lepidoptera pupae are gregarious, and a succession of adults emerge through one or a few emergence holes (Figs 84, 85). Only rarely is staining seen.
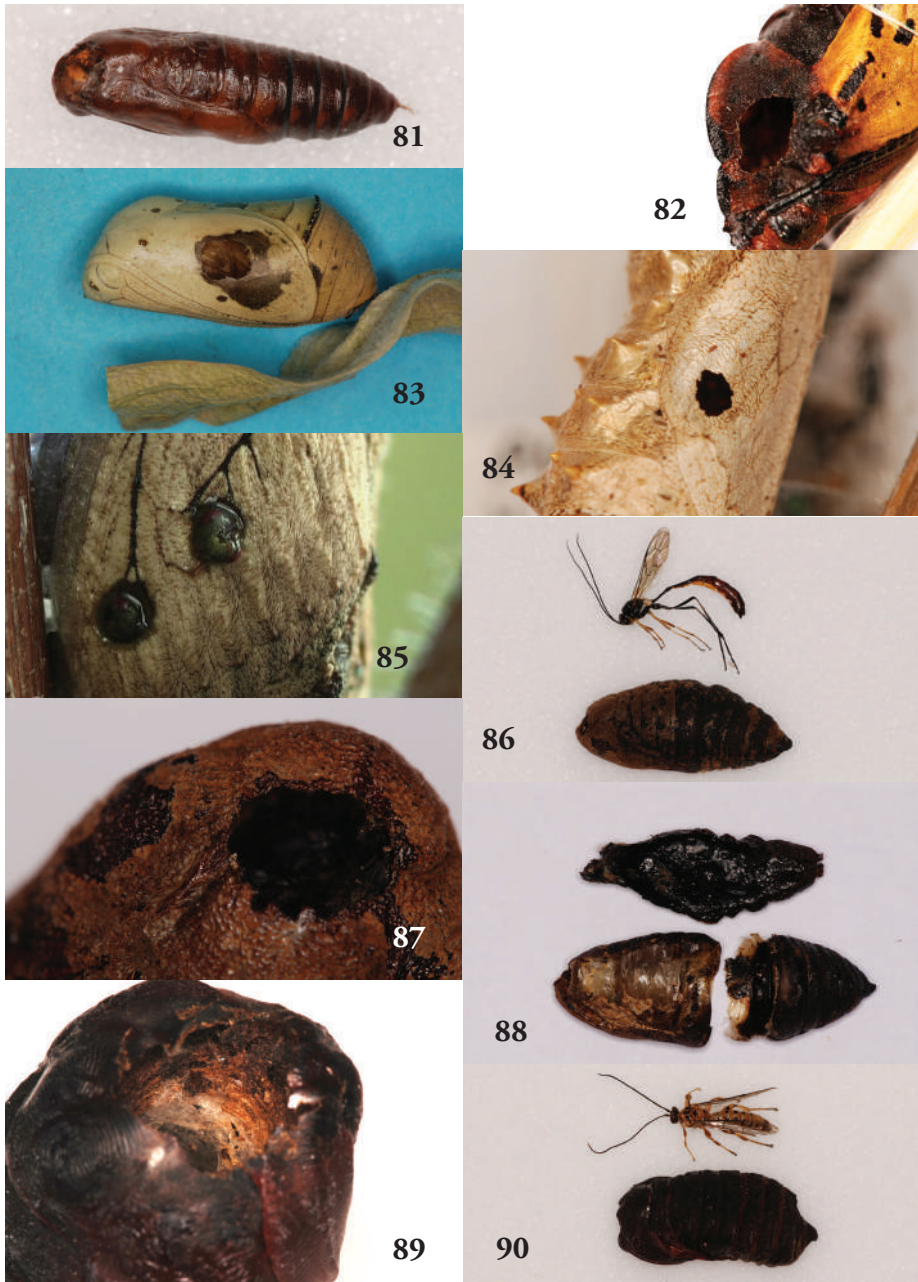
Figure 81–90. 81 *Dusona admontina* (Speiser) from *Herminia grisealis* (Dennis & Schiffermüller) (Erebidae) **82** *Brachymeria tibialis* (Walker) from *Aporia crataegi* (Linnaeus) (Pieridae) **83** *Brachymeria albicrus* (Klug) from *Danaus chrysippus* (Linneaus) (Nymphalidae: Danainae) **84, 85** *Pteromalus puparum* (Linnaeus) **84** from *Aglais urticae* (Linnaeus) (Nymphalidae) **85** emerging from *Papilio machaon* Linnaeus (Papilionidae) **86–88** *Agrypon* sp. from *Copaxa multifenestrata* Herrich-Schäffer (Saturniidae) **88** showing host residue removed from its pupa **89, 90** *Xanthopimpla* sp. from *Attacus atlas* (Linnaeus) (Saturniidae). The figures are not all to the same scale (applies to all plates).

Discussion

Quite apart from the video evidence (*Trogus lapidator* 1st emerging – 16 September 2013; https://www.youtube.com/watch?v=GrhKhsj00BE and *Trogus lapidator* 2nd emerging - 16 September 2013; https://www.youtube.com/watch?v=y_p8QcnHgjs) and Figs 1–4, it is seen from the host remains through which *Trogus* and the closely related *Psilomastax* have emerged long before (Figs 5–9) that the pupal cuticle has been degraded by a wet substance, not only because of the 'molten' appearance around the edges of the emergence hole but also because it is more or less extensively stained. Unsurprisingly, papilionid pupae in BMNH from which *Holcojoppa* species (another *Trogus*-subgroup genus) have emerged have the same appearance (G. Broad, pers. comm.). We have observed generally sharper edges to the emergence holes of other ichneumonids, but staining would be expected to be less noticeable in the tough dark brown (subterranean) pupae typical of many large moths. Despite a moderate incidence of staining (see below), especially in Ichneumoninae, we have searched hard to see damage comparable with that caused by the *Trogus*-subgroup but have found very little sign of it elsewhere, even in the same tribe Heresiarchini (Figs 10–12) or in the relatively tough and often pale-coloured pupae (many of which are exposed and sometimes of long duration) of many butterflies from which a variety of ichneumonids have emerged. Thus we conclude that in general emergence from host pupae depends, as the existing perception has it, essentially on the action of the adult parasitoid's mandibles, and that the *Trogus*-subgroup is exceptional. However, elsewhere in Ichneumoninae staining is rather widely seen, especially in some of the lighter-coloured butterfly pupal remains examined, such as *Nymphalis polychloros* (Linnaeus) parasitized by *Hoplismenus terrificus* (Wesmael) (Figs 13, 14), and some (Fig. 15) (but not all; Fig. 16) *Coenonympha pamphilus* (Linnaeus) parasitized by *Hoplismenus bispinatorius* (Thunberg), as well as in several *Ichneumon* species (Figs 18, 21, 23–25) although again without consistency (compare Figs 25 and 26). There are also a few weak examples from Listrodromini (Figs 38, 40). It is hard to be absolutely dismissive of the possibility of help from biochemicals in view of these clear signs of rather even staining around the edges of the emergence hole, especially in cap-cutting taxa. On the other hand, both in Ichneumoninae and in other subfamilies, it is possible that this can arise coincidentally (Fig. 40 shows an unusually stained *Celastrina argiolus* (Linnaeus) parasitized by *Lystrodromus nycthemerus* (Gravenhorst), with numerous others being free of staining; and Fig. 59 is the only example seen of staining in Anomaloninae, affecting only one area of the pupa of *Zegris eupheme* (Esper) from which *Clypeocampulum lubricum* (Atanasov) has emerged). While staining may result only incidentally, for there are always liable to be fluids accompanying the emergence of parasitoids (see Fig. 85, showing fluid in the hole being chewed by *Pteromalus puparum*, despite the typically clean appearance of the hole left in the (different) pupal cuticle once dry in Fig. 84), it points to a possibly interesting study awaiting anyone with the necessary patience, or luck, to investigate these phenomena in action. Chalcididae often leave strong stains behind them (Fig. 83) but this may just represent excess fluid consequent on their unusually small size in relation to the size of the pupa parasitized. The state of the host

when arrested by the parasitoid is another factor likely to have a bearing on staining, as it might be expected that histolysed hosts could potentially leak quite a lot of fluid during parasitoid emergence, and in a rather inconsistent way.

Overall, even from this very sparse survey within a narrow zoogeographical region, there is considerable evidence that the form, toughness, concealment and duration of the host pupa plays a major role in determining how specialist ichneumonids emerge from it, although the trends within and between ichneumonid tribes and subfamilies outlined above might repay a more detailed and wider survey. While the toughness of the host pupa correlates quite strongly with its duration, and the strongest pupae tend to be cap-cut, there is not complete correspondence (for example, *Agrypon polyxenae* ecloses by chewing a hole (Figs 61, 64) in very tough exposed pupae that must persist unprotected for ten or more months in the field). In the subfamily Ichneumoninae both koinobiont and idiobiont taxa are found, but there seems to be no consistent difference in the mode of emergence between them, although we have had fewer examples of the latter category to explore.

It is rather obvious that some correlation between mandibular structure and the kind of exit holes made would be expected, and indeed this is rather easily seen — *Trogus*, in particular, has quite small coarsely punctate but otherwise unremarkable mandibles; the teeth are blunt and although the upper tooth is the larger the two teeth are in the same plane. But it is well beyond the scope of the present paper to attempt more than cursory notes on variation in mandibular structure in relation to eclosion, especially bearing in mind the minimal extent of the data. Also, the mandibular structure of the Chalcidoidea mentioned is fundamentally different from that of ichnemonids and cannot be compared. Nevertheless it seems clear that the best cap-cutters in the Ichneumonidae (e.g. Listrodromini (Figs 38–40), *Hoplismenus* (Figs 14–16) and *Eurylabus* (Fig 54), as well as some *Ichneumon* and close relatives) have a relatively long and acute upper tooth and a reduced and sometimes inflexed lower tooth; and some of the crudest emergence holes are made by the taxa with untwisted mandibles and the least difference in size of the two teeth, such as *Goedartia* (Fig. 55) and *Pimpla* (Fig. 74). Even within a genus, such as in *Ichneumon* (Figs 17–29), this trend appears to hold up moderately well. However, it is not always the case: for example the phaeogenine *Herpestomus brunnicornis* (Gravenhorst) has the sharp upper tooth substantially the longer and yet exhibits predominantly type 2 emergence (Fig. 42). Another phaeogenine, *Heterischnus*, shows a consistent detaching of an apicoventral cap (Fig. 43), presumably in some way connected with its strongly curved, narrow and unidentate mandibles. Among Anomaloninae, the type 1 cap-cutting taxa seem to have the upper tooth on the whole slightly longer than in the hole-chewing taxa, and perhaps more particularly to have a stronger flange along the lower margin of the mandible. For some taxa, evolutionary pressure on the form of the mandible to enable emergence from the host's substrate (or cocoon) must trump the barrier of the mere host pupal cuticle. This presumably accounts for the form of the widened blunt mandible of *Chasmias* and the crudity with which it leaves the host (Figs 36, 37) en route to chewing through a tough plant stem. Another case is the mess made of the host pupa (Fig. 56) by *Cotiheresiarches*

before it tackles the hard cocoon of its host; in this case the whole face is unusual, with a protruding plate-like clypeus as well as blunt, unidentate and curved mandibles, which presumably aid its escape from the host's tough obovoid cocoon through a small circular hole (much as that made by the moth when it emerges, and possibly exploiting the same prepared facility; the cocoon in Fig. 56 has been artificially torn open). For others, such as Pimplini, not much specialisation of the rather broadly tapering and small toothed subequidentate mandible for eclosion seems to have occurred, although the arguably most specialised genus of those examined, *Apechthis*, which tends to cut strips (visible in both Figs 72 and 73) and emerges from relatively neat holes, does have an out-turned lower rim of the mandible if not quite a flange. An interesting difference is seen in the two species of *Metopius* examined (Figs 70 and 71), which belong to two subgenera with significantly different mandibular structure. Although *Metopius* (*Peltocharus*) *dentatus* (Fabricius) (Fig. 70), which has a tough host cocoon in addition to its pupa to contend with, has a slightly longer upper tooth the two teeth are in the same plane, while in *M.* (*Tylopius*) *leiopygus* Foerster (Fig. 71) the mandible is twisted, with the small lower tooth inflexed, so that the mandibles present as scissor-like blades. This brief survey by no means covers the range of mandibular structure seen in Ichneumonidae, and in fact most of the truly bizarre structures known in the family are not included, although probably most have nothing to do with Lepidoptera pupal hosts. Nevertheless, it seems clear that among taxa eclosing from Lepidoptera pupae there are strong links between the form of the mandibles and the kind of egress opening that is made, allowing also for any need to break through whatever additional protection the host pupa may habitually have, with some predictive possibilities. The extent to which these characteristics have evolved to meet (sometimes extreme) autecological requirements, rather than being rooted in phylogeny, is an unresolved question of a familiar kind, but the more that is understood about the basic biology of the host-parasitoid relationships the better such conundrums can be resolved.

The origin of the presumed secretion through which the host pupal cuticle is degraded by the eclosing *Trogus* adult is unknown. Although it would not explain how the necessary agent reaches the site of emergence, it would be worth investigating whether the extremely coarsely sculptured metasomal tergites of the *Trogus*-subgroup (which are unlike those of other ichneumonines, and whose morphology appears not to have been explained) may have a glandular, secretory function, as it is difficult to see what other (externally visible) morphological feature of *Trogus* might be involved, although its mandible is unusually coarsely punctate. Otherwise, the glossa and other submandibular aspects of the mouthparts seem rather enlarged in *Trogus*, but this might be a modification for merely spreading the fluid.

As an extension of this survey, we examined extralimital pupae of very large saturniid moths from which rather smaller solitary ichneumonids had emerged, on the one hand an unidentified koinobiont *Agrypon* (=*Trichionotus*) species (Anomaloninae) from a Mexican saturniid, *Copaxa multifenestrata* Herrich-Schäffer (Figs 86–88), and on the other hand an unidentified idiobiont *Xanthopimpla* sp. (Pimplinae) from *Attacus atlas* (Linnaeus) in Thailand (Figs 89, 90). In the first (*Agrypon*) the *Copaxa*

pupa was very malodorous some days after after the parasitoid's emergence, and when opened (Fig. 88) the now-hard but messy remains of the host (apparently very unstructured; probably fully histolysed) could be seen to have been separated (perhaps within a membrane) from the area that had been occupied by the pupating parasitoid, which did not appear to have been isolated from them by any clear cocoon and may have resided in the ecdysal space of the host pupa. The staining seen in Fig. 87 seems more likely to have been a result of incidental spillage from wet host content than to indicate biochemical degradation of the host pupal chitin. In the case of *Xanthopimpla* the parasitoid appeared to have scraped its way through considerable distances of accreted material in the *Atticus* pupa, leaving a more or less smooth tunnel through a very hard substance, without resulting in any clear staining of the cuticle (Fig. 89) that might have indicated biochemical assistance (although most of its arduous journey to the surface did not involve the host cuticle, *Xanthopimpla* has basally broad but evenly narrowed mandibles which are strongly twisted so that the small ventral tooth is not involved in the powerful pickaxe-like anterior presentation). In contrast to the smelly *Copaxa* remains, those of the *Attacus* were set hard and (at least by the time they were received by MRS) inoffensive with a faintly sweet smell, perhaps indicating that some suppression of microorganisms had occurred, possibly in the manner reported for *Pimpla* by Führer and Willers (1986). But whether or not pimplines such as *Pimpla* and *Xanthopimpla* may provide interesting antibacterials, they do not seem to degrade chitin or other impediments to adult emergence biochemically.

It should be noted that no consideration has been given here to emergence of adult Ichneumonidae through the host pupal (or puparial) cuticle of Diptera (e.g. as by Diplazontinae which have specialized mandibles: Rotheray 1981), or the *Orthocentrus*-group of Orthocentrinae (in which mandibles are severely reduced).

Acknowledgements

References

Diller E, Shaw MR (2014) Western Palaearctic Oedicephalini and Phaeogenini (Hymenoptera: Ichneumonidae, Ichneumoninae) in the National Museums of Scotland, with distributional data including 28 species new to Britain, rearing records, and descriptions

of two new species of *Aethecerus* Wesmael and one of *Diadromus* Wesmael. Entomologist's Gazette 65: 109–129

Fürher E, Willers D (1986) The anal secretion of the endoparasitic larva *Pimpla turionellae*: sites of production and effects. Journal of Insect Physiology 32: 361–367. doi: 10.1016/0022-1910(86)90049-1

Rotheray GE (1981) Emergence from the host puparium by *Diplazon pectoratorius* (Gravenhorst) (Hymenoptera: Ichneumonidae), a parasitoid of aphidophagous syrphid larvae. Entomologist's Gazette 32: 39–41.

Sanetra M (1998) *Trogus lapidator* (Fabricius, 1787) (Hymenoptera: Ichneumonidae) aus einer Puppe von *Papilio alexanor* Esper, 1799 (Lepidoptera: Papilionidae) sowie weitere Parastoide. Nachrichten des Entomologischen Vereins Apollo (NF) 19: 269–270.

Shaw MR, Bennett FD (2001) Host prepupal mummification by *Colpognathus* Wesmael (Hymenoptera: Ichneumonidae, Ichneumoninae). Entomologist's Gazette 52: 201–203.

Sime KR, Wahl DB (2002) The cladistics and biology of the *Callajoppa* genus-group (Hymenoptera: Ichneumonidae, Ichneumoninae). Zoological Journal of the Linnean Society 134: 1–56. doi: 10.1046/j.1096-3642.2002.00006.x

Wahl DB, Sime KR (2006) A revision of the genus *Trogus* (Hymenoptera: Ichneumonidae, Ichneumoninae). Systematic Entomology 31: 584–610. doi: 10.1111/j.1365-3113.2006.00329.x