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Biological and morphological studies on the parasitoids (Hymenoptera, Ichneumonidae) of *Aprosthema tardum* (Klug) (Hymenoptera, Argidae, Sterictiphorinae) in Var, southern France

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Abstract

Field surveys at four neighbouring but discrete sites in southern France revealed the presence of five ichneumonid parasitoids of the *Lathyrus*-feeding sterictiphorine argid sawfly *Aprosthema tardum*. Four of these parasitoids, *Lathrolestes erythrocephalus*, *Ischyrocnemis goesi* (both Ctenopelmatinae), *Terozoa quadridens* and *Thibetoides aprosthemae* (both Tryphoninae), could be identified and, by also incorporating laboratory studies, the developmental biology of each was elucidated and illustrated. A little supplementary information from a site in Italy is also presented. The fifth species was detected only once and failed to develop in its cocoon; it remains unidentified but the cephalic sclerites of its final instar larva are illustrated. The identified parasitoids are all more or less rare and little-known species and prior to this study only *L. erythrocephalus* had a known host; the others were biologically unknown even at the generic level and not recorded from France. The egg of *L. erythrocephalus* bears prominent hooked structures at its capital end, not reported in other studied *Lathrolestes* species. From its biology as an endoparasitoid of a sawfly and from larval characters, *Ischyrocnemis* is confidently assigned to Ctenopelmatinae. Both ctenopelmatines could successfully parasitise the host during any of its 2nd to 5th instars, but the tryphonines were less flexible. *Terozoa* monitors hosts until the moult to the final instar before ovipositing on them, usually affixing the egg to the head and often an eye (stemma), while *Thibetoides* parasitises much younger hosts, placing its strongly anchored egg behind a thoracic leg where it remains through successive host moults. Some characters used in the past to determine *Terozoa* species are discussed, and a new provisional key to the known species of *Terozoa* is presented. The very different developmental biology

of *Terozoa* and *Thibetoides* may challenge views that they are closely related genera. *Terozoa bituberculata* (Constantineanu, 1973), **stat. rev.** is raised from synonymy with *T. quadridens* Perkins, 1962. Reinterpretations of several cephalic structures of final instar larvae as well as larval spiracles are discussed, and a new interpretation and terminology for describing the latter is introduced.

Keywords

Classification, Ctenopelmatinae, developmental biology, egg, egg position, *Ischyrocnemis goesi*, larva, larval cephalic sclerites, *Lathrolestes erythrocephalus*, morphology, phenology, spiracles, *Terozoa* key, *Terozoa quadridens*, *Thibetoides aprosthemae*, Tryphoninae

Introduction

The tenthredinoid sawfly family Argidae contains around 972 world species as recognised by Taeger et al. (2018) and is regarded as one of the most basal groups of tenthredinoid sawflies (Nyman et al. 2019). It is a largely tropical and east Asian group, but 64 species occur in Europe arranged in the two currently recognised subfamilies (Malagón-Aldana et al. 2022): Arginae, dominated by the genus *Arge* Schrank (29 European species); and Sterictiphorinae comprising the genera *Sterictiphora* Billberg (9 species) and *Aprosthema* Konow (24) (cf. Fauna Europaea, consulted 12.iv.2020).

In Europe the genus *Arge*, with several rather common species feeding on trees and shrubs, is well-known to have an extremely specialised and taxonomically isolated parasitoid fauna, including the braconid *Proterops nigripennis* Wesmael (Ichneutinae), the ichneumonids *Boethus thoracicus* (Giraud), *Eclytus* (*Anoplectes*) *multicolor* (Kriechbaumer) (both Tryphoninae) and *Scolobates auriculatus* (Fabricius) (Ctenopelmatinae), the chalcidid *Conura xanthostigma* (Dalman) (Chalcidinae), and the tachinid flies *Belida angelicae* (Meigen) and to a large extent *Vibrissina turrita* (Meigen) (both Exoristinae) (Pschorn-Walcher and Kriegel 1965; Schedl and Pschorn-Walcher 1984). The above Hymenoptera are all the only species of their genera or (in the case of *Eclytus*) subgenera in Europe, except for *Scolobates* which has four additional, less widely distributed, native congeners (one of which, *S. nigerrimus* Ulbricht, has also been recorded from *Arge*; cf. Aubert 2000), and another apparently recent arrival reared in Sweden from *Arge pullata* (Zaddach) (Anderbrant and Broad 2019). The tachinid genera *Belida* and *Vibrissina* each have one other European species. In addition, some species in much larger chalcidoid genera with wide overall host ranges also specialise on *Arge* species (e.g. the gregarious eulophids *Tetrastichus atrocoeruleus* (Nees) and *T. hylotomarum* (Bouché) (Noyes 2019)).

The comparatively good knowledge of these uncommon or rare parasitoids of *Arge* species owes as much to their host larvae feeding on trees and bushes as to the abundance of some *Arge* species, thus being relatively easy to find, collect and rear. European species of Sterictiphorinae, on the other hand, have been far less studied in respect of parasitism (cf. Pschorn-Walcher and Altenhofer 2000), only one species of *Sterictiphora* (*S. geminata* (Gmelin) on *Rosa*) being widespread and sometimes abundant, although *Aproceros leucopoda* on *Ulmus* is a recently invasive species (Blank et al. 2010).

Parasitoids of *S. geminata* are not mentioned in either of the main published studies of that species (Beneš 1968; Scheibelreiter 1972), although Zwakhals and Blommers (2022) have recently recorded a specimen of the tryphonine ichneumonid *Neleges proditor* (Gravenhorst) reared from it in the Netherlands; the first host record for the genus. Otherwise, larval parasitoids of Sterictiphorinae in Europe appear to be very poorly, if at all, known. The largely Palaearctic genus *Aprosthema* comprises generally rare and taxonomically difficult species (e.g. Vikberg 2004) feeding on herbaceous Leguminosae (Fabaceae), but they have seldom been reared and, again, almost nothing is known of their parasitoids (cf. Pschorn-Walcher and Altenhofer 2000).

In parts of Var (S. France) one species, *Aprosthema tardum* (Klug), has proved to be quite widely distributed and not uncommon, feeding on the widespread *Lathyrus latifolius* in a variety of biotopes (Liston et al. 2018). Following the chance discovery of a cocoon from which a tryphonine ichneumonid emerged, that proved to be a new species *Thibetoides aprosthemae* Shaw (Shaw et al. 2018), considerable efforts were made by PK and BKvLS to collect larvae of *Aprosthema* in order to try to investigate this parasitoid further, as nothing was hitherto known about the biology of the rare genus *Thibetoides*. Gradually, as other parasitoids of *Aprosthema* were found, the project grew into an investigation of their biology as well, but at no time did we seek to provide a quantitative analysis of the parasitoid complex – partly because we were forced to use some of the wild-collected larvae of *Aprosthema* for experimental manipulations rather than rearing each one (only late in the project, from early 2020, were we able to obtain a culture of *A. tardum* from eggs). Instead, we have simply concentrated on elucidating and filming as much of the biology, and resolving the taxonomy, of each parasitoid species as we could.

In the course of this investigation, ongoing since 2014, three further species of very poorly known Ichneumonidae were also reared from, and often found in the act of parasitizing, the *Aprosthema* species of this study, and aspects of their life histories were filmed. These species are *Lathrolestes erythrocephalus* (Gravenhorst), *Ischyrocnemis goesi* Holmgren and *Terozoa quadridens* Perkins. There is a single published rearing record for the first of these, from an undetermined *Aprosthema* sp. in Kazakhstan (Reshchikov 2015), but there are no published biological data of any kind for the other two. This paper describes the biology of all four of the parasitoids identified, and suggests an appropriate subfamily placement for the enigmatic genus *Ischyrocnemis* Holmgren from unequivocal biological evidence.

Material and methods

Field sites

Although a small number of *Aprosthema* larvae were collected from additional sites nearby, there were four main sites (Fig. 1) in Dracénie Provence Verdon (Var, France) from which this study stems. Some are rather diffuse but each is believed to support an essentially self-contained population, more or less isolated (or at least discontinuous) from those in the other areas.

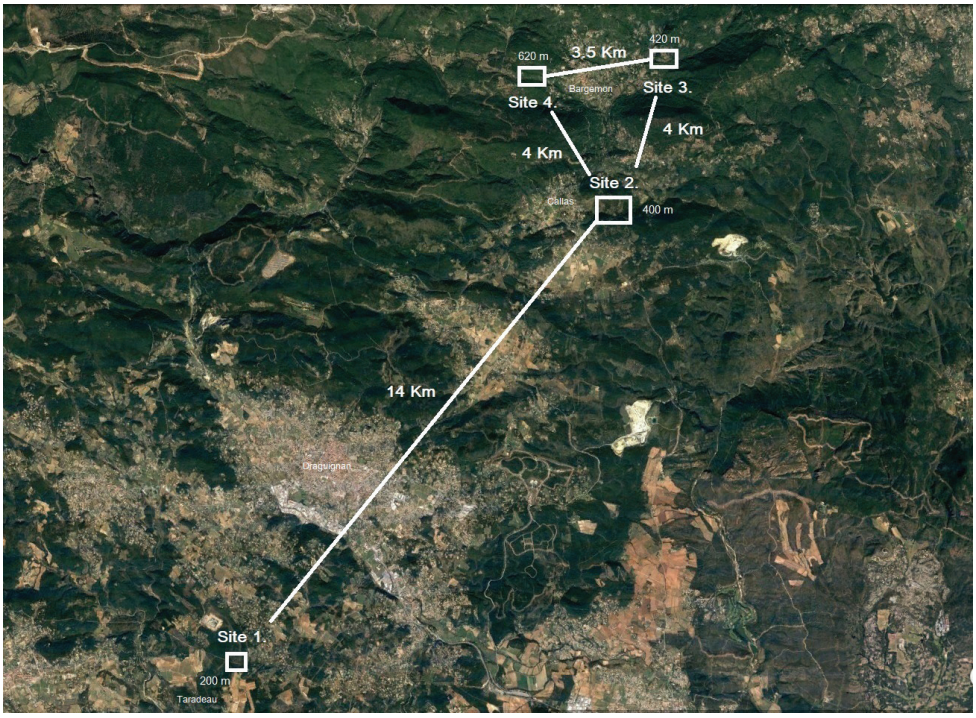


Figure 1. Aerial photograph of the main collecting area in Var, with principal sites and altitude overlayed.

Site 1. Taradeau (200 masl; N 43.2931, E 6.2555). A rather small area comprising a linear fire-break of slightly disturbed limestone grassland and scrub (half of the approximately 25 m wide strip being mown along its 350 m length in alternate winters), within a moderately open mixed dry forest.

Site 2. Callas, Colle Blanche (400 masl; N 43.3519, E 6.3328). Along a forest road (900 m × 10 m) through *Pinus* and *Quercus* with intermittent open spaces. A nearby similar road on the same slope of Colle Blanche at Clavier is included. Also, La Garidelle, a nearby open mixed forest with fields and forest roads; although there were many host plants, only one larva was found in 2016 and none in 2017 and no further effort was made.

Site 3. Bargemon, Les Estangs (420 masl; N 43.3721, E 6.3435). A large (5 hectares) and very diverse wild garden with ponds and hedgerows, in 300 × 50 m of which *Lathyrus* grows. The forest road leading to it (Le Plan) with many roadside *Lathyrus* plants is included (a strip of approximately 50 × 5 m).

Site 4. Bargemon, Favas (623 masl; N 43.3714, E 6.3149). An abandoned clearing, measuring about 200 m × 50 m, along a road, with numerous shrubs surrounded by *Quercus* and *Pinus*.

Other sites involved in the study included: (i) Le Muy. A wooded area along a road between vineyards where many *Lathyrus* plants grow. A number of larvae were collected but were unable to form their cocoons, possibly owing to the use of

insecticides, so parasitism was not ascertained. The site was visited only once, in 2018, and is not considered further. (ii) Apricale, Italy (302 masl; N 43.5342, E 7.3906), which is a wild garden in an olive grove with many *Lathyrus* plants, surrounded by a mixed forest of *Quercus*, *Castanea* and *Pinus*. Although this place is almost 100 km from the locations in Var, the similar findings from small collections made there are also presented.

Although *L. latifolius* is certainly the dominant *Lathyrus* in the region, on which the vast majority of the *Aprosthema* collected had undoubtedly fed, the scarcer but closely similar *L. sylvestris* has also been recorded locally and we cannot discount the possibility that larvae may sometimes have been collected from that. The two plants are not easy to tell apart, and no effort was made to do so.

Sampling

All field-work (2014–2020) was conducted by PK and BKvLS. In the early years it was focussed on ascertaining the identity of the cocoon from which *Thibetoides aprosthemae* was reared in 2014 (Shaw et al. 2018), and larvae of *Aprosthema tardum* were first found in 2016. The first parasitoids were not reared from hosts known at the time of collection to be *A. tardum* until 2017. From 2018 to 2020, the four main locations were visited regularly every week (1 to 3 times for between one and four hours), from the middle of March to the first week of August. Adults of *A. tardum* emerge from around the middle of March and larvae appear in the field from mid-April continuously until about mid-July. After then larvae were no longer found in the field, although at a much-reduced level some cultured larvae continued developing successfully until mid-August, then producing only over-wintering cocoons.

No formal sampling protocols were employed; rather, collections were opportunistic and approaches adjusted when new observations and questions arose. For much of the period covered by this paper the host was not very numerous and many tens of hours were spent searching in each year. Binoculars (Pentax 6.5 × 21 Papilio II) were often used to search plants for characteristic signs of feeding in order to protect the sites from trampling. Although cocoons were always collected when found, not all encountered larvae of *Aprosthema* were collected immediately: the locations of some of the smaller ones were marked with a view to collecting the larvae at a later stage, with varying levels of success. Some of the host larvae we collected were reared in a straightforward way, but others were used for experiments with parasitoids. Most of the adult *A. tardum* reared were returned to their site of origin.

Collections made

The total numbers of host larvae and cocoons found at the four principal sites, and at Apricale, are presented in Table 1. Effort was broadly similar for Site 1 for all years and at other principal sites in the three years 2018–2020, so those totals at least roughly reflect the considerable fluctuations in the host populations over the period.

Table 1. Numbers of immature *Aprosthema tardum* larvae, and additionally summer cocoons in parentheses, seen at the main sites. Sites 2, 3 and 4 were not visited as frequently in 2016 and 2017 as in following years. In 2016 and 2017 all larvae were collected, but in 2018–2019 a proportion of the younger larvae were left, to be collected when more mature (with varying recovery). All 36 cocoons were collected as soon as found.

SITES	2016	2017	2018	2019	2020	Total
Site 1	6	12	6 (1)	39 (3)	2	69
Site 2	2	-	32 (2)	11	61	108
Site 3	2	1	39 (13)	23	17 (2)	97
Site 4	1	0	5 (4)	24 (7)	41 (3)	85
Apricale	-	(1)	0	5	5	11
	11	**14**	**102**	**112**	**131**	**370**

Rearing

Host larvae in their fourth and fifth instars (i.e. within 6 days of forming a cocoon) were reared individually in 9 cm diameter × 14 cm tall glass containers closed with a screwed lid, with freshly cut sections of *Lathyrus latifolius* (which stays fresh under these conditions for about seven days). Details of their progress were recorded daily. Four days after becoming cocooned, they were individually removed to a 1 × 9.5 cm glass tube closed with cotton wool.

Second and third instar larvae were treated similarly except that the *Lathyrus* was stood in a buried pot of water with a cylinder inverted over it. Cocoons were kept under conditions of natural light, and as far as possible kept outdoors and shaded.

Experimental exposure to parasitoids

While some observations were made (and even filmed) in the field, much of the behavioural information on the parasitoid species, and most of the filming, was obtained indoors in front of a large closed window to facilitate recovery of the parasitoid adult. Host larvae were always offered in their feeding positions on foodplant. The adult female parasitoids involved were either reared or collected in the field; in either case they were fed on dilute honey and also given flowers.

Preserveration of adult parasitoids

Except for a small number of specimens of *L. erythrocephalus* deliberately selected for dissection (see below) all adult parasitoids were killed by placement in a domestic freezer (ca -20 °C) for about an hour, then transfer to 96% ethanol for shipment to Edinburgh.

Dissections

Dissections (in water) of both adult female parasitoids and *Aprosthema* larvae to recover parasitoid eggs or 1st instar larvae were performed on material preserved in 70%

ethanol in France then sent to Edinburgh. Minor distortions (and changes in appearance of egg content, in particular) inevitably will have taken place.

DNA sequencing

In order to provide a basis for future phylogenetic analysis of the reared parasitoids, some of which are very rarely encountered, we sequenced the D2 and partial D3 segments of 28S rRNA (28S) and the "barcoding portion" of cytochrome oxidase subunit 1 (CO1). DNA extraction and sequencing followed standard protocols, as detailed in Johannson and Klopfstein (2020). The sequences are available in Genbank under the accession numbers recorded under each of the determined parasitoid species here. The relevant specimens are deposited in the National Museums of Scotland (NMS) and labelled accordingly.

Preparation of final instar larval heads

Methods of preparation are those of Wahl (1989). The measurements of the labial sclerite and mandible use the landmarks in Finlayson (1975: figs 2 and 4). DBW's notation for larval preparations follows the museum acronym: it consists of his initials, the day, month, year, and a letter designating the individual preparation. The terminology for the cephalic sclerites of the mature larva is that of Wahl (1990) and Sime and Wahl (1998). A new terminology for spiracles is included in the Discussion.

It should be noted that almost all drawings of ichneumonid cephalic sclerites will involve elements of reconstruction, due to vagaries of the mounting process which can result in tears, skewing of sclerite positions, and structural distortions. The method employed by DBW, here and elsewhere, is to use a drawing tube to make accurate outlines, and then flip and trace structures so as to produce a bilaterally symmetrical result, which aims to be a faithful rendition of the original. For this study, setae have been placed to accurately reproduce their position and number.

In a series of papers culminating in Short (1978), J.R.T. Short described and drew the final instar cephalic sclerites of a wide range of Ichneumonidae. This was pioneering work, but unfortunately Short's drawings are often at odds with the original slide mounts in terms of proportions and details. His drawing methodology is unknown, although he may have used an ocular grid. Reinterpretations of some of his slides are presented.

Photography

The associated videos were filmed using a Canon XL2 with a 20× zoom, XL 5.4–108 mm lens, supplemented when appropriate with the addition of a Canon 72 mm close-up 500D lens. For macro a Canon EF 100 mm 1:2.8 with an EF Canon XL adaptor was used. The footage is recorded on mini DV tapes of 60 minutes. Photos of living insects were taken in the field with a Lumix HD Panasonic DMC-TZ10 or

abstracted from the filmed sequences. Photos of eggs and early instar larvae obtained by dissection were taken as single shots down one arm of a Wild M5A binocular microscope with ×20 eyepieces using a Canon PowerShot S110. Photos of mounted adults are stacked. DBW's images of cocoons and whole larvae were taken with an EntoVision micro-imaging system, consisting of a Leica M16 zoom lens attached to a JVC KY-75U 3-CCD digital video camera that feeds image data to a desktop computer. The program Archimed 5.3.1 was used to merge an image series (representing typically 15–30 focal planes) into a single in-focus image. Lighting was provided by an EntoVision dome light. Photographs of larval slides were taken by a Nikon D810 body attached to a Nikon Labophot compound microscope with a trinocular head; photograph series were assembled into a single image using Helicon Focus 7.6.4 Lite.

Determinations and depositories

Aprosthema tardum was initially determined by Andrew D. Liston. Material is deposited in NMS and Senckenberg Deutsches Entomologisches Institut (**SDEI**). All parasitoids were determined by MRS and are mostly deposited in NMS, with the following exceptions: One female of *Terozoa quadridens* has been donated to each of Canadian National Collection of Insects (**CNC**), Zoologische Staatssammlung München (**ZSM**) (especially to enable both sexes of *T. quadridens* and *T. anatolica* to be compared within the ZSM collection), and Natural History Museum London (**NHMUK**). One female of *Ischyrocnemis goesi* has been donated to NHMUK. Slides of larval preparations were examined from National Museum of Natural History, Smithsonian Institution (**NMNH**), Utah State University Collection (**EMUS**) and Australian National Insect Collection, CSIRO (**ANIC**).

Terminology

We use the term "plurivoltine" to indicate that a species has more than one generation per annum, i.e. that it does not have a fully obligatory diapause but rather can develop successive generations in a season. Often it may in practice be largely bivoltine, but the term plurivoltine allows for the possibility that under favourable circumstances there may be more than two annual generations to a significant extent.

Results

The host and its biology (Figs 3–9) (FilmingVarWild video 1)

Liston et al. (2018) described and illustrated the biology of *Aprosthema tardum*; minor additions are given in the following summary. There are five larval instars and, in line with other investigated Argidae (Kontuniemi 1965), there is no post-feeding instar for cocoon construction. The winter is passed as a cocooned prepupa. At relatively low altitude and in years with an early spring, up to four partly overlapping generations per

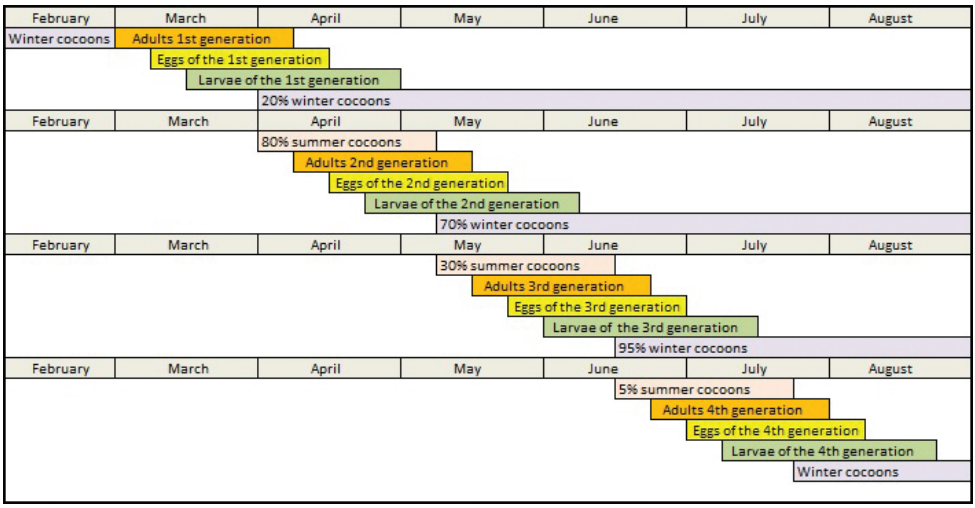
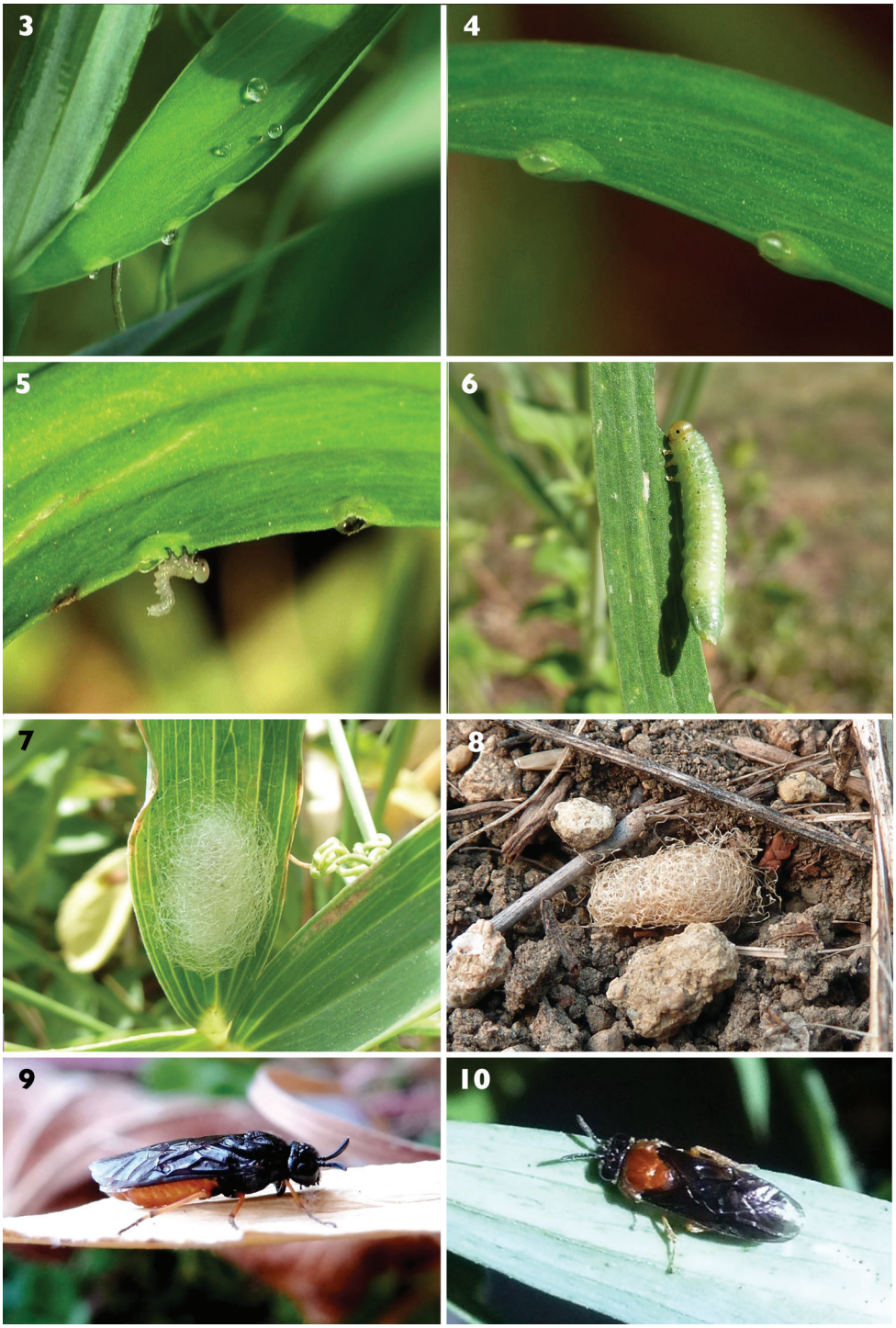


Figure 2. Flow chart showing approximate phenology of *Aprosthema tardum* at 200–400 m in Var. Underlying data come from both field observations and captive breeding. The timings depicted are for an early spring, and will vary according to temperature: in cool years or following a late spring and at the higher altitude sites there may be only three rather than four partial generations. Depending on season and weather, adult females generally live for 7–10 days; eggs take from 5–14 days to hatch; larval life occupies 10–18 days; and adults emerge from summer cocoons after 7–12 days.

annum can occur (Fig. 2), with first generation adults (i.e. emerging from overwintering cocoons) first appearing in early March. No adults of *A. tardum* were seen visiting flowers. From observations on released adults, which initially fly (in ascending circles in the case of males) to the canopy, it is presumed that courtship and mating take place there: this assumption was reinforced by the observation of a dead male in a spider's web at 3 m height. Females were regularly observed among the foodplant, but on only two occasions did we see a male, in each case briefly approaching an ovipositing female but without success. We were unable to induce mating in captivity. If constrained, captive virgin females commence oviposition after about 24 hours, and continue to do so without deviation if released. The egg is placed between the upper and lower epidermis of leaves of *Lathyrus latifolius* (Fig. 3); generally two eggs are deposited per leaf, but sometimes more. Depending on weather, the early spring eggs develop in around 14 days but, as the season progresses, this can be in as little as five to six days. One or two days before the egg hatches, the area in the leaf edge becomes conspicuous owing to the development of the relatively large first instar larval head (Fig. 4).

The first instar larva (Fig. 5), which immediately starts feeding at the leaf margin, is about 3 mm in length. By its final instar the larva feeds across the width of the leaf, leaving a characteristic stepped profile. The larvae move little: sometimes the entire larval development takes place from a single leaf. After about 10–18 days and four moults the fully fed final instar larva (Fig. 6) measures about 11–14 mm (males) to 14–17 mm (females).

An important feature is the clear difference in cocoon structure and positioning of overwintering cocoons ("winter cocoons") from those from which adult sawflies will



Figures 3–10. *Aprosthema* species **3–9** *Aprosthema tardum* **10** unidentified *Aprosthema* species **3** eggs in situ **4** eggs soon before hatching **5** newly hatched 1st instar larva **6** 5th instar larva **7** summer cocoon **8** winter cocoon **9, 10** adult female.

emerge in the year of formation ("summer cocoons"). Summer cocoons (Fig. 7) are constructed among more or less aerial vegetation, though often somewhat concealed from view. They have a coarse open weave and are rather springy, and pale yellowish in colour. The winter cocoon (Fig. 8, showing a cocoon constrained to be spun exposed) is made in or just below the litter layer. While still having a more or less open weave it is denser and generally smaller (about 10–13 mm as opposed to 12–15 mm), almost hard owing to its much thicker (almost wiry) strands, and usually darker (buff or light brownish). Both morphs have a thin more densely spun inner envelope, that of the summer cocoon being still somewhat open, but more parchment-like in the winter version. In practice it is immediately obvious from its construction whether or not a cocoon is destined to overwinter. As expressed in Fig. 2, an increasing proportion of the cocoons made in each generation comprises winter cocoons, thereby entering diapause in summer. Emergence from summer cocoons takes 7–12 days. A total of 33–36 days development from oviposition to adult for the non-diapausing fraction of the second generation (i.e. first complete cycle of the season) is typical, but summer development in the following generation may take less than 30 days.

Differences in the head morphology of adults of winter and summer generations are rather pronounced, particularly in females, and similar to the dimorphism described by Vikberg (2004) in *Aprosthema melanurum* (Klug) (Liston et al. 2018). As noted by these authors this is a reflection of the relatively tougher winter cocoon, necessitating stronger musculature for the mandibles, which are larger in the winter generation although there is no major difference in their structure between generations. The colour of the adult (Fig. 9) is fairly constant.

A second possible host (Fig. 10)

Some way into this research we discovered that a second species of *Aprosthema*, probably undescribed (Andrew Liston, pers. comm.), also feeds on *Lathyrus* in the area, but it is evidently present in very much smaller numbers. We observed (but could not collect) one female in the act of oviposition at Site 2 in 2018, and reared another female (Fig. 10) from a summer cocoon collected at Site 4 in 2019, in contrast to the roughly 100 adults of *A. tardum* reared from larvae and cocoons collected in the field. No differences were noted among the *Aprosthema* larvae collected, but it seems likely that any differences between the two species would be slight and easily overlooked: however, it should be noted that we have not seen a larva known to belong to the second species (unfortunately the tagged plant on which oviposition was observed had been destroyed by wild boar by the time of our next visit). For the purpose of this paper we are treating all the parasitoids reared as using *A. tardum*, and additionally presuming that the second species is also parasitized equally; i.e. quantitative statements do not distinguish between the two. Although any rearing from wild-collected larvae or cocoons unfortunately cannot be fixed to either of the possible hosts with certainty on morphological grounds, some experimental rearings of parasitoids using male *A. tardum* larvae resulting from known and certainly determined virgin females have provided unequivocal host associations of *L. erythrocephalus*, *I. goesi* and *T. quadridens* with *A. tardum*. Adult females

of the two *Aprosthema* species differ conspicuously in colour (Figs 9, 10) and also in a range of morphological features, but the (as yet undecided) identity of the second species is under investigation by A. D. Liston and is not further considered here.

Parasitism

No parasitoid taxa ovipositing into the cocoon (as opposed to the larva) were found (36 summer cocoons collected overall) and, rather surprisingly, no evidence of parasitism by Tachinidae (Diptera) was seen. Four species of Ichneumonidae that could be identified to species were found, all of which attack the larval stage, are strictly solitary, and emerge as adults from the host cocoon. A fifth species (henceforth Ctenopelmatinae sp. X) was detected only from a single cocooned prepupa resulting from a host larva collected at Site 2.

Table 2. Presence of parasitoids detected at the various sites. Note that collecting intensity was relatively low in the years 2016–2017, and at Apricale. *Thibetoides aprosthemae* was also found at Site 1 in 2014, which stimulated this study.

	Lathrolestes erythocephalus	*Terozoa quadridens*	*Thibetoides aprosthemae*	*Ischyrocnemis goesi*	Ctenopelmatinae sp. X
Site 1					
2016	✓	-	-	-	-
2017	-	-	-	-	-
2018	✓	✓	-	-	-
2019	✓	✓	✓	-	-
2020	✓	-	-	-	-
Site 2					
2016	✓	-	-	-	-
2017	-	-	-	-	-
2018	✓	✓	-	✓	✓
2019	✓	✓	-	✓	-
2020	✓	-	-	-	-
Site 3					
2016	-	-	-	-	-
2017	-	-	-	-	-
2018	✓	✓	-	-	-
2019	✓	✓	✓	-	-
2020	✓	✓	-	✓	-
Site 4					
2016	-	-	-	-	-
2017	-	-	-	-	-
2018	✓	✓	-	-	-
2019	✓	✓	✓	-	-
2020	✓	✓	-	-	-
Apricale					
2016	-	-	-	-	-
2017	-	-	-	-	-
2018	-	-	-	-	-
2019	✓	-	✓	-	-
2020	-	-	-	-	-

The sites in which the parasitoids are known to have been active are recorded in Table 2. Given that the only years of intensive sampling were 2018–2020, it is clear that the most abundant parasitoid, *Lathrolestes erythrocephalus*, was universally and consistently present (also occurring at Apricale). The next most regularly recorded (although comparatively rare) parasitoid, *Terozoa quadridens*, occurred at all four of the main sites and was found in all of them in most years. The other two regular parasitoids were found only in smaller numbers, but *Thibetoides aprosthemae* was present at three sites (and additionally at Apricale) and *Ischyrocnemis goesi* at two. Discounting the unidentified Ctenopelmatinae sp. X, only Site 3 was found to support all four of the other parasitoid species, though (sometimes different) combinations of three species were present at the other main sites. The taxonomy, biology and phenology of each parasitoid species is outlined in separate sections below.

***Lathrolestes erythrocephalus* (Ctenopelmatinae, Perilissini)**
Figs 11–28; FilmingVarWild videos 2, 3, 10–13

Taxonomy. *Lathrolestes* is a medium sized genus with about 25 European species, remarkable among Ctenopelmatinae for including parasitoids of leaf-mining Lepidoptera and (outside Europe) Coleoptera (Barron 1994) in addition to the otherwise apparently universal parasitism of Symphyta by the subfamily (Broad et al. 2018). There is no controversy concerning the identity of *L. erythrocephalus*, which is a distinctive species (Figs 11, 12). In contrast, its generic placement is less certain. Much of the literature, including most databases, has placed it in *Perilissus* Holmgren, 1857, but Aubert (2000) transferred it to *Lathrolestes* Förster, 1869 and the most recent taxonomic revision (Reshchikov 2015) of *Lathrolestes* included *erythrocephalus*. On the grounds that this is the latest generic placement in a formal taxonomic work, we follow that here, despite the more numerous previous references to it as a species of *Perilissus* (in which genus it might arguably have best been left pending a more thorough and wider review (Gavin Broad, pers. comm.)). The phylogeny of Ctenopelmatinae is beyond the scope of this paper but, because *Perilissus* as currently construed is almost certainly polyphyletic, arguing for a simple return of *erythrocephalus* to that genus would not constitute a real advance. It is the type species of the genus *Polyoncus* Förster, 1869, currently

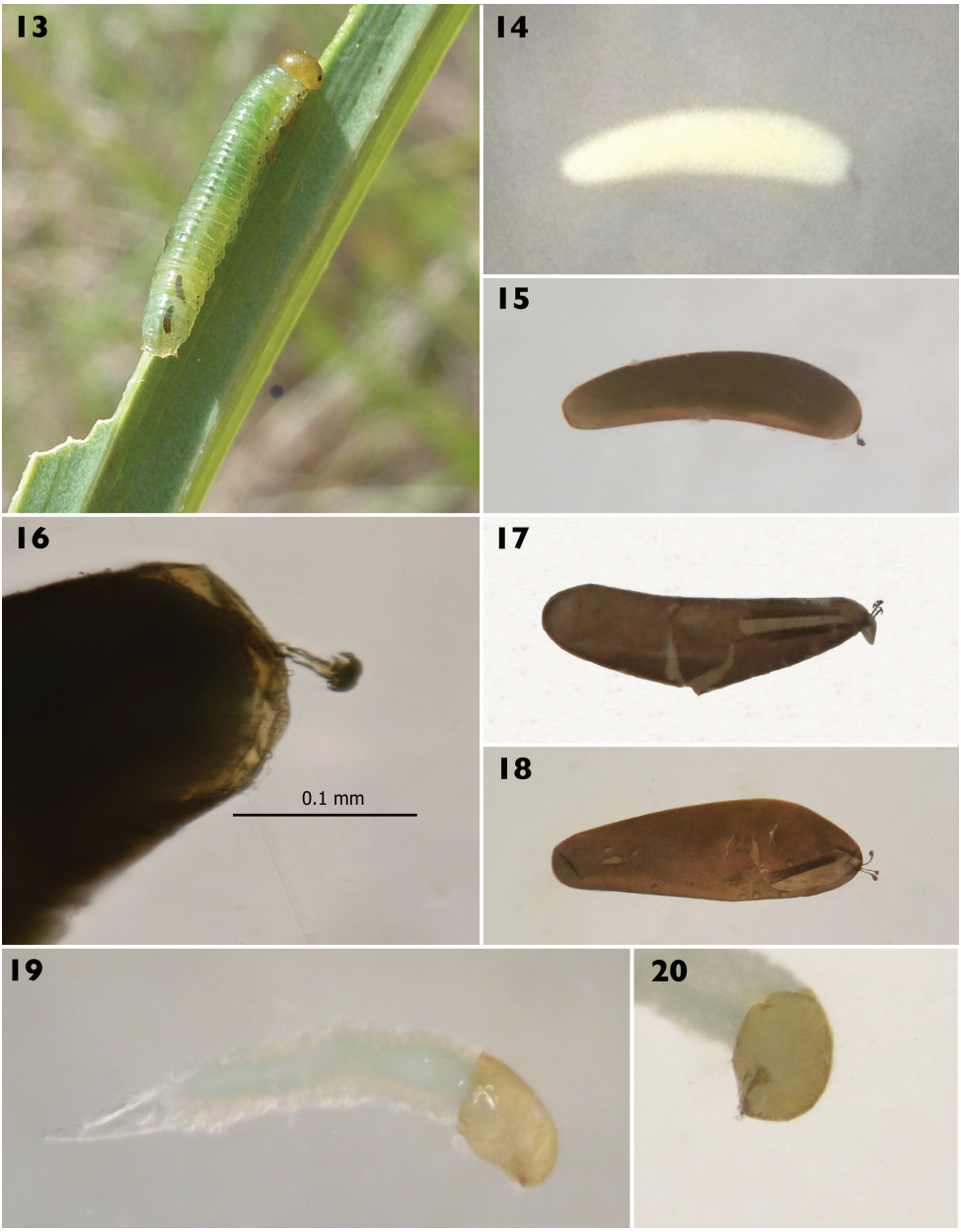
Figures 11, 12. Female *Lathrolestes erythrocephalus* **11** alive **12** mounted.

regarded as a synonym but which might one day be resurrected. *Lathrolestes erythrocephalus* (as *Perilissus*) has previously been recorded from France, and Reshchikov (2015) cited a rearing record from an undetermined *Aprosthema* species in Kazakhstan.

Genbank accession numbers of *L. erythrocephalus* from our study (SK_19_50): CO1 OK393909; 28S OK393942.

Biology. This is by far the dominant species in the parasitoid complex of *A. tardum*, consistently present at all well-sampled sites including Apricale (Table 2) and having several, probably overlapping, generations through the season. Over 40 have been reared from wild-collected hosts (plus many more in culture). The earliest date of emergence from a winter cocoon was 7 March. Adults were regularly encountered in the field, searching the *Lathyrus* plants from late March to the end of July, especially in somewhat overcast weather. Its distinctive dark eggs were seen in many host larvae in the field, from their second instar onwards, often more than one in a host (Fig. 13). Although the hatched eggshells remain visible, the growing host becomes progressively more opaque and this external sign of parasitism is less evident in the late instar hosts. In experiments *L. erythrocephalus* freely oviposited into 2nd to 5th instar larvae, with successful outcome from each instar. As also observed in the field, often more than one egg was laid in a host during essentially the same visit to a well-grown larva, which seemed deliberate, and in cases of separated visits or successive visits by different females we saw no avoidance of either superparasitism or multiparasitism. After brief antennal exploration that seems to be of the recent feeding damage as much as of the host itself, oviposition takes from 7 to 28 seconds; the host, especially when large, sometimes reacts by raising its abdomen and thrashing, but smaller hosts are more often unreactive. The host is not temporarily paralysed and, during oviposition, the female parasitoid is in contact with it only by its ovipositor. On one occasion a female *L. erythrocephalus* was seen to bite and eat most of an early instar *Aprosthema* larva, this destructive event being the only host-feeding seen.

Dissections showed that freshly emerged females (N = 2) have no mature eggs in the common oviduct, but after 4 days with access to dilute honey there are usually about 20, with more to come (N = 4). The initially white egg, ca 0.75 × 0.18 mm (Fig. 14), darkens within two or three hours of being laid (Fig. 15), eventually to become practically black. It bears a remarkable hooked terminal protrusion, probably in fact a set of protrusions (Figs 15–18), unequivocally deduced to be at its head end from four lines of evidence: (i) the position of these hooks at the broader end of the egg (Figs 14, 15); (ii) the consistent appearance of hatched eggshells recovered by dissection (Figs 17, 18); (iii) dissection of a well-developed but dead ruptured egg found in a host, probably killed by a competing first instar larva, in which the head capsule was discerned at the end with the hooks, and the caudal appendage was seen to be curled under (or possibly over) the posterior segments at the other pole; and (iv) the orientation of the egg as it leaves the ovary such that the narrow (unadorned) caudal end passes into the oviduct first in accordance with Hallez's Law (Hallez 1886), confirmed by dissection of a 4 day-old female with mature eggs present in the common oviduct. Once in the host's haemocoel the toothed protrusions seem to act as grappling hooks to weakly fasten the egg to a tissue such as the gut or muscle following free (random)

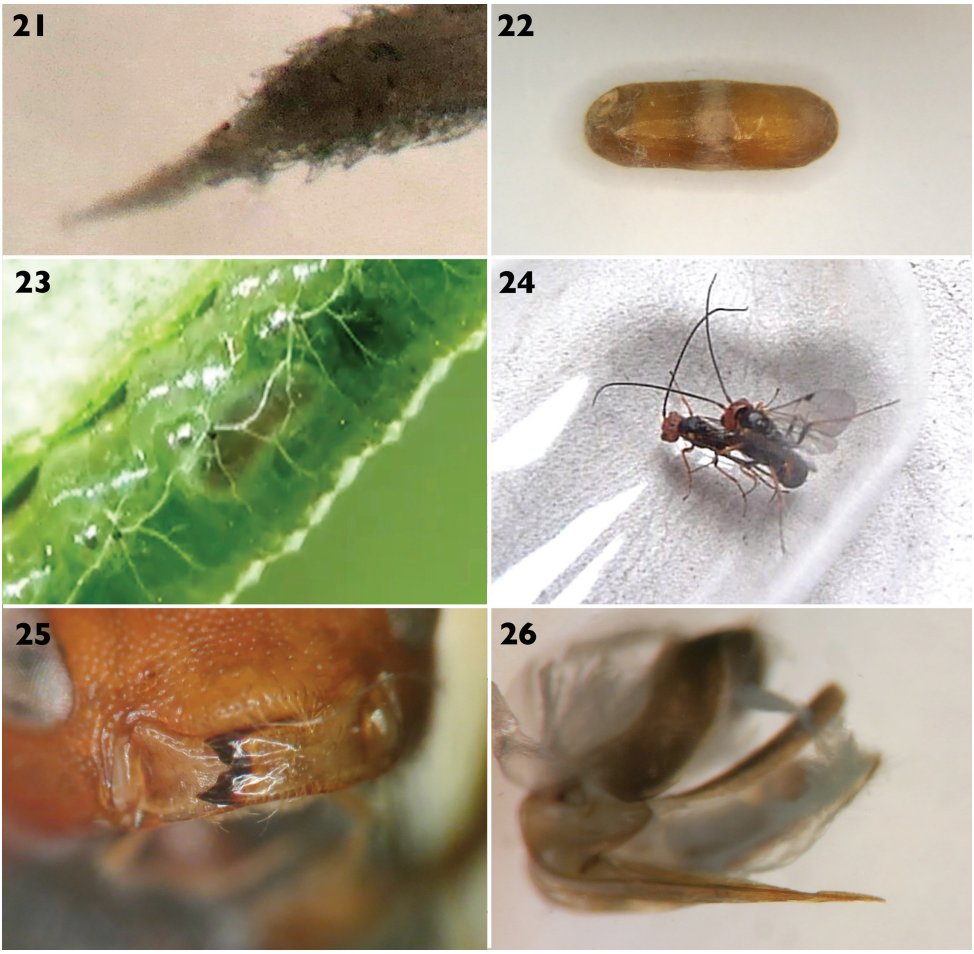


Figures 13–20. *Lathrolestes erythrocephalus* **13** clear view of two of the four eggs present in a 4th instar *Aprosthema tardum* larva **14–18** egg, dissected from host **14** freshly laid [fuzziness is photographic artefact] **15** preserved about three hours after being laid **16** detail of hooks at anterior end **17–18** chorion after hatching **19–20** first instar larva **19** habitus **20** head to show mandibles.

placement. The egg hatches on the third day and the caudate first instar larva (Fig. 19) leaves the chorion completely, and measures ca 1.2 mm. It has large sharp mandibles (Fig. 20) and weak (easily overlooked) ventrolateral tooth-like projections particularly

on the more posterior abdominal segments (Fig. 21). It can often be seen through the host's integument as it moves freely within the host's body and it has sometimes been observed apparently re-visiting its own eggshell, perhaps as part of a routine inspection to eliminate competitors using its sharp mandibles. The larva stays in its first instar until the host is cocooned. After then completing its feeding rapidly, it makes its orange-brown weakly banded cocoon (Fig. 22) inside that of the host.

Generally the adult parasitoid emerges during the summer from summer cocoons of the host, after about 26 days, and often it will overwinter in the host's winter cocoon, but this phenological relationship is evidently not under endogenous control as the parasitoid has often emerged in the same summer from an intended winter host cocoon, or sometimes during the winter when hosts would be unavailable. Several



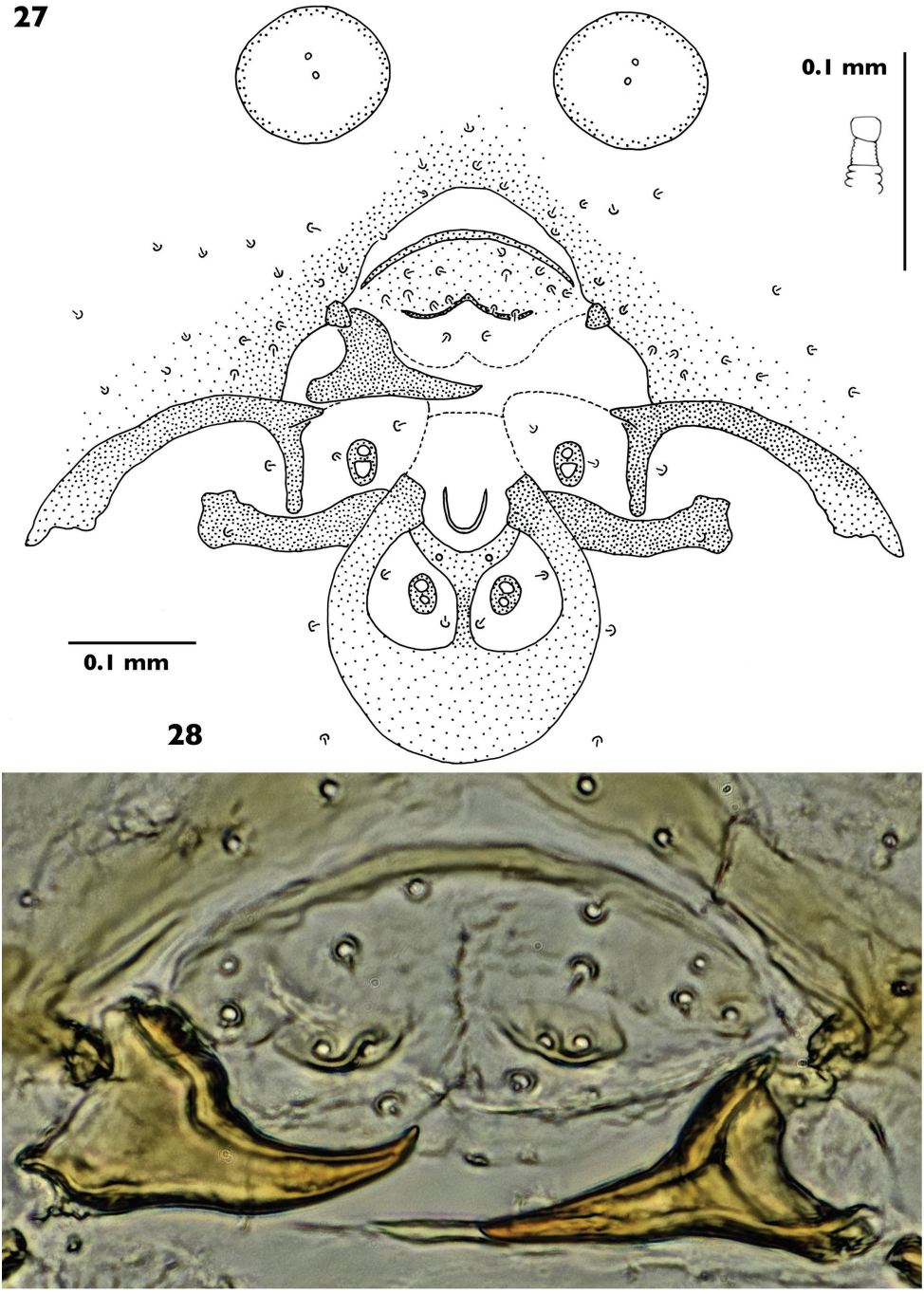
Figures 21–26. *Lathrolestes erythrocephalus* **21** posterior ventrolateral abdominal segments of first instar larva to show ventrolateral protrusions. **22** cocoon **23** encapsulated egg in *Aprosthema tardum* larva **24–26** adult **24** mating **25** mandible **26** ovipositor (dissection).

times it has remained in its cocoon within a winter host cocoon through the following summer to emerge later (this happened in several cases, emergence eventually being prompted following an airline flight to Edinburgh and a period of darkness then subsequent indoor warmth in the early part of the next winter): presumably, left to themselves, in both the foregoing cohorts these adults would usually have emerged in spring, having skipped a year, although in two cases we have witnessed emergence in late September and early October, at a time when no hosts would be present, from undisturbed cocoons made in June and July of the previous year. It is difficult to ascribe this entirely to captive conditions. Sometimes the host successfully encapsulated a *L. erythrocephalus* egg (Fig. 23) and developed to the adult stage, which could be construed as evidence that the very frequently observed self-superparasitism may be adaptive in significantly improving the likelihood of success (see Discussion). We observed a single copulation in captivity, with the stance (Fig. 24) permitting antennal contact typical of many Ichneumonidae (cf. Shaw et al. 2021). Morphological features of mandibles, briefly discussed later, and ovipositor are given in Figs 25 and 26 respectively.

In several cases of observed multiparasitism, the faster-developing *L. erythrocephalus* generally triumphed over both *Thibetoides aprosthemae* and *Terozoa quadridens*; though sometimes the host was unable to moult successfully when parasitised by both *T. aprosthemae* and *L. erythrocephalus*, with the result that host and parasitoids all perished. Adults of *L. erythrocephalus* successfully developed on several occasions following oviposition by *I. goesi* into *A. tardum* larvae in which *L. erythrocephalus* had already been present, but the reverse situation was not investigated.

Final instar cephalic sclerites (Figs 27, 28). ***Specimens examined*****:** DBW 14.vi.2020d, 27.vi.2020a, 27.vi.2020b, 27.vi.2020c, 27.vi.2020d, 13.vii.2020b, 13.vii.2020c, 13.vii.2020d (all NMS).

Cephalic structures generally moderately to strongly sclerotized. Epistoma lightly sclerotized; epistomal band present; dorsal margins of both poorly defined and merging with general light sclerotization of frons. Labral sclerite absent; clypeolabral area with lightly sclerotized central region, lenticulular in shape, with moderately sclerotized dorsal margin, bearing setae and two clypeolabral plates next to its ventral margin. Stipital sclerite present and strongly sclerotized, more or less horizontal; cardo absent. Pleurostoma lightly to moderately sclerotized; posterior struts of inferior mandibular processes not connected by band; accessory pleurostomal area weakly present; lateral margins of pleurostoma and pleurostomal area weak and fading into general cephalic area. Hypostoma long and strongly sclerotized, lateral end not divided in two at posterior tentorial pit and without extensions; accessory hypostomal area present on dorsal margin and lightly sclerotized. Hypostomal spur present, about 2.5–2.9 × as long as its basal width. Labial sclerite weakly ovoid, lightly to strongly sclerotized. Salivary orifice U-shaped. Prelabial sclerite present as weakly sclerotized transverse band, connected to interior ventral margin of labial sclerite by weakly sclerotized projection of labial sclerite. Labial sclerite with 6 setae. Prelabial area with 4 setae. Maxillary and labial palpi each bearing two sensilla. Mandible strongly sclerotized; blade about 0.6 × as long as full mandibular length, without fine denticles. Antenna without papillus.



Figures 27, 28. *Lathrolestes erythrocephalus*, cephalic sclerites of final instar larva **27** drawn **28** photographic detail.

Parietal band present as lightly to moderately sclerotized vertical oblong with irregular margins. Spiracle with closing apparatus absent; intercalary trachea absent, subatrium about as long as atrium. Skin covered with small, bubble-like protuberances; spines absent; setae present, short and scattered.

As noted below under Ctenopelmatine species X, Short's (1978) key to tribes of ctenopelmatine larvae is woefully inadequate. But, as discussed in the *Ischyrocnemis goesi* section below, there are a number of ctenopelmatine genera that have a clypeolabral structure that superficially resembles a labral sclerite: *Lathrolestes*, *Opheltes*, and *Perilissus* in the Perilissini, *Euryproctus* in the Euryproctini, and *Protarchus* in the Mesoleiini. Short (1978) illustrated *Lathrolestes luteolator* (Gravenhorst) as having this structure, and it is interesting that *L. erythrocephalus* has it as well. Unfortunately, Short's characterization of *Lathrolestes* is at odds with what is presented here for *L. erythrocephalus*: he states the labial sclerite is ventrally incomplete and the epistomal band absent ('Median dorsal part of the epistoma not lightly sclerotized'). Perhaps his interpretation was due to a poor preparation: examination of Short's slides reveals many of the heads to be essentially dismembered or twisted about, resulting in partly imaginative illustration.

Perhaps the most surprising finding was the lack of a spiracular closing apparatus. The other two ctenopelmatines in this study lack it as well. Short (1978) illustrates 57 ctenopelmatine species, with the spiracle shown in 55 of them; of these 55, only six were depicted as lacking the closing apparatus. DBW has been able to examine 16 of Short's original Ctenopelmatinae slides that were deposited in NMNH: Euryproctini (*Hypsantyx lituratoria* (Linnaeus), *Phobetes striatus* (Davis), *Synodites olympiae* (Ashmead), *Synomelix* sp.); Mesoleiini (*Lamachus albopictus* Cushman, *L. contortionis* Davis, *L. eques* (Hartig), *L. lophryii* (Ashmead), *L. ruficoxalis* Cushman, *L. tsugae* Cushman, *L. virginianus* (Rohwer), *Mesoleius tarsalis* (Cresson), *M. tenthredinis* Morley); Perilissini (*Lophyroplectrus nipponensis* Cushman, *Opheltes glaucopterus flavipennis* (Provancher)); Pionini (*Rhorus clapini* (Provancher)), for all of which Short portrayed a closing apparatus; but re-examination showed that only two (*Synomelix* sp. and *Rhorus clapini*) actually had one. Finlayson (1960a, 1960b, 1963) illustrated the spiracles of eight species of *Mesoleius* and *Lamachus* and all also lack a closing apparatus. It would appear that this condition is quite widespread among ctenopelmatines. A number of other subfamilies of higher Ophioniformes appear to lack the closing apparatus as well, although in a different way: Ophioninae, Campopleginae, and Cremastinae (DBW, pers. obs.). Elucidation of exactly what is going on in these endoparasitoids will require further study (see also Discussion).

***Ischyrocnemis goesi* (Ctenopelmatinae)**
Figs 29–41; FilmingVarWild videos 4, 12

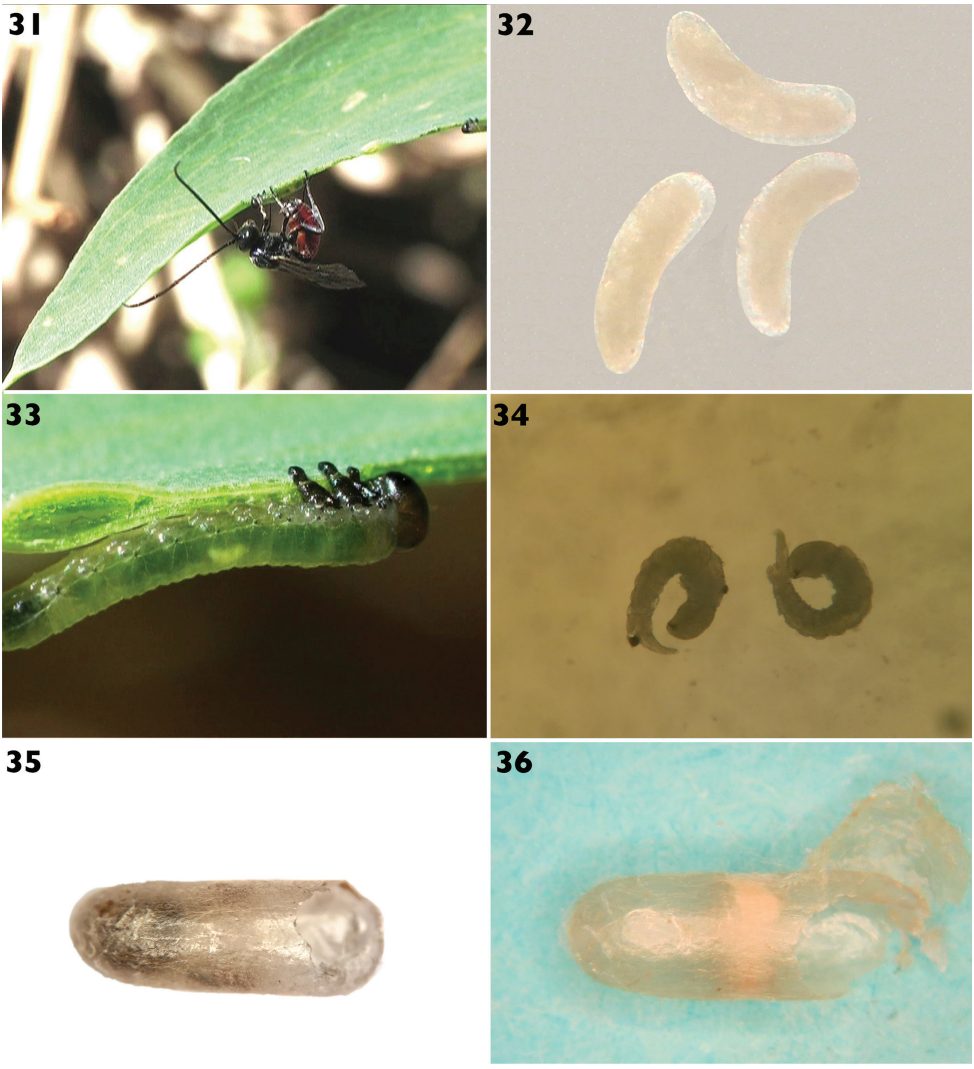
Taxonomy. (See also section on *Terozoa*, below). *Ischyrocnemis* has been variously treated as a member of Ctenopelmatinae (Perkins 1962; Townes and Townes 1959) or Metopiinae (Townes 1971; albeit doubtfully), and both Perkins (1962) and Aubert (2000) suggested it might best be placed in the ctenopelmatine tribe Pionini by envisioning a relationship with *Rhorus* Förster, 1869. Nevertheless, its placement, even to subfamily, has remained

Figures 29, 30. *Iscyrocnemis goesi* female **29** in life **30** mounted.

problematical and has not been resolved by molecular and morphological phylogenetics (Quicke et al. 2009), although the biological evidence presented here comes down firmly in favour of Ctenopelmatinae. Whether the uncertainty has been compounded by the confusion between *Ischyrocnemis* (Ctenopelmatinae) and *Terozoa* (Tryphoninae) is unclear but possible. The two were regarded as synonyms since Townes (1971) [despite Perkins 1962] until Kasparyan (2019a) resolved the matter. At species level our determination of *I. goesi* is based on the key to the five Eurasian species given by Kasparyan (2019a), of which only *I. goesi* is known in Western Europe. It has not previously been recorded in France.

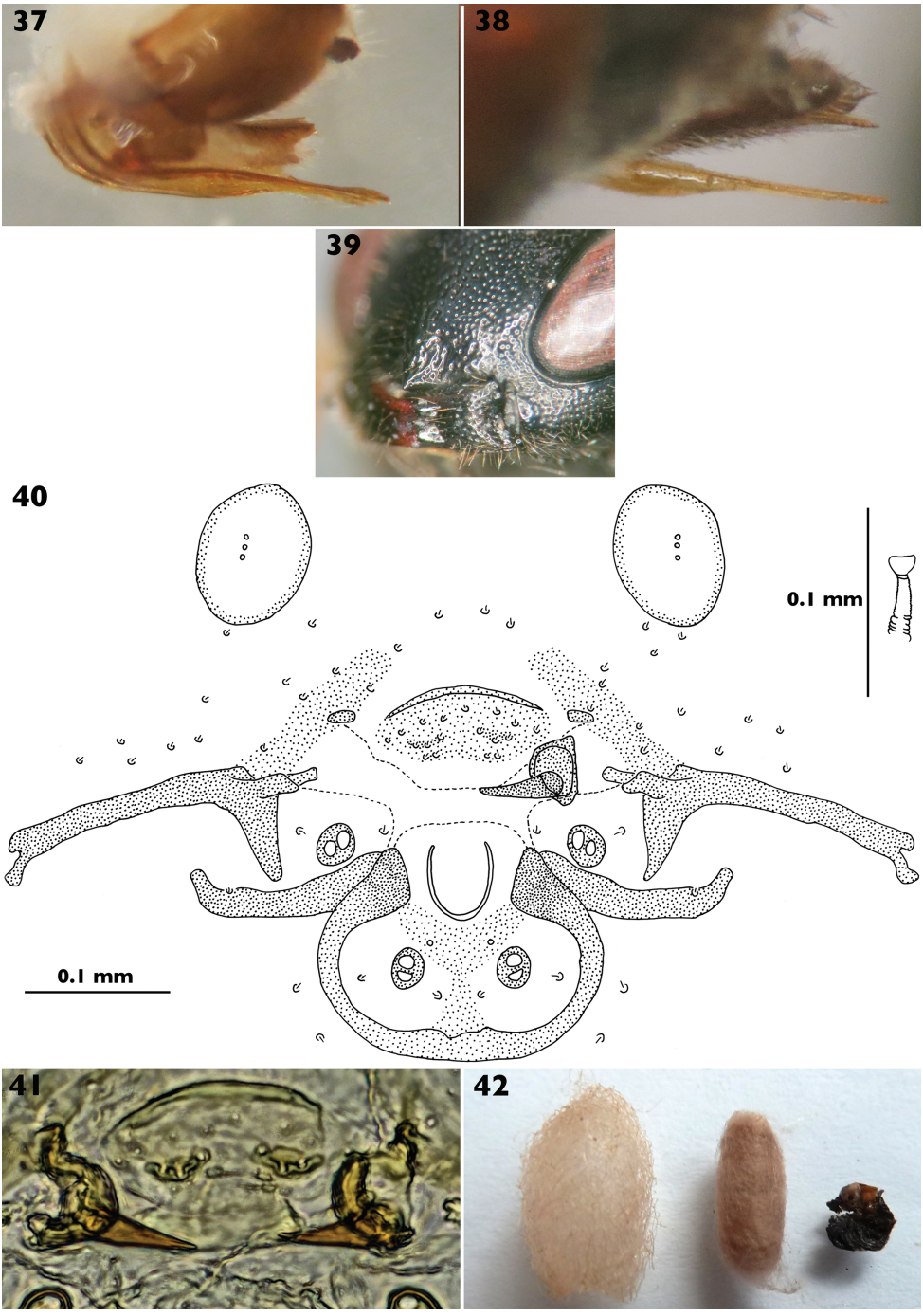
Genbank accession numbers of *I. goesi* from our study (SK_19_49): CO1 OK393908; 28S OK393941.

Biology. *Ischyrocnemis goesi* (Figs 29, 30) was found at just two sites (Table 2) and only in small numbers. It was only ever reared from winter cocoons (N = 7), from host larval collection dates 8–13 June with host cocoon formation 14–20 June, and emergence of the adult parasitoid 3–18 April the year after. It was reared in culture only twice (both from winter cocoons, following oviposition into late instar hosts on about 26 June with emergence of one adult male on 11 May the next year, and a female that died failing to eclose at about the same time) from several ovipositions into unparasitized hosts in captivity. Most of these hosts, readily oviposited into from 2nd to 5th instars, unfortunately died as prepupae in host winter cocoons (never in summer cocoons), or sometimes as larvae before cocooning. The capture of two adult females in the field, on 12 May and 25 June, on the face of it might suggest that *I. goesi* is plurivoltine, but we have not been able to show that, neither from field rearings nor experimentally, and it seems more plausible that it is univoltine and that either there is a prolonged emergence period from winter cocoons (cf. 3–18 April and also 11 May, above) and/or the adult females are unusually long-lived. It is possible that oviposition by *I. goesi* provokes the host into forming a winter cocoon, but the evidence is only circumstantial. Oviposition takes place after only brief antennal contact with the host, which is usually grasped by at least the front two pairs of legs during a process lasting from 7–22 seconds (Fig. 31). The ovipositing female orientates along the long axis of the host, but both head-to-head and head-to-tail orientations were seen and the egg is randomly placed in the haemocoel. There is no paralysis, but the host generally fails to react until later.



Figures 31–36. *Ischyrocnemis goesi* **31** ovipositing into 2nd instar *Aprosthema tardum* **32** three eggs dissected from a superparasitised host **33** recently laid egg in 2nd instar host **34** two first instar larvae dissected from a superparasitised host **35, 36** cocoon.

The small white egg is about 0.4 × 0.11 mm long, strongly curved, and without any appendage (Fig. 32). In small hosts it is visible through the cuticle (Fig. 33), and remains white until the caudate first instar larva hatches within 3 days. On dissection from the host the first instar larvae seen were curled (Fig. 34) but if arranged straight would be about 1.1 mm long (including tail) with a large head (about 0.2 mm long) soon after hatching, in overall appearance typical of many endoparasitoid ichneumonids. We could not detect any sign of a surrounding trophamnion, although from the relative sizes of freshly laid egg and first instar larva the possibility that the egg is alecithal should not be ruled out. The larva probably remains in its first instar until the



Figures 37–42. 37–41 *Ischyrocnemis goesi* **42** Ctenopelmatinae sp. X. **37, 38** ovipositor **37** dissected **38** dry mount with valves separated (lower ones exposed) **39** apex of clypeus and mandible **40, 41** cephalic sclerites of final instar larva **40** drawn **41** photographic detail **42** cocoon and host remains removed from host cocoon.

host has formed its cocoon, though we did not ascertain that. The first instar larvae depicted in Fig. 34 were dissected from a single host and the dark material adhering to the left hand larva might be a result of its having been wounded by the other. The frail parchment-like cocoon is light brown with its strong central band frequently orangish (Figs 35, 36). The ovipositor is shown in Figs 37 (dissection) and 38 (valves separated in dead specimen). The apex of the clypeus bears a pronounced tooth, and the teeth of the broad mandible have internal flanges (Fig. 39).

Although self-superparasitism is easily induced in captivity (cf. Figs 32, 34), it seems not to be deliberate and requires successive visits (though these can be almost immediate). On one occasion a male *I. goesi* was reared from a host carrying three *Terozoa quadridens* eggs when collected.

Final instar larval cephalic sclerites (Figs 40, 41). ***Specimens examined*****:** DBW 17.vi.2020b, 17.vi.2020a (both NMS).

Cephalic structures generally moderately to strongly sclerotized. Lateral portions of epistoma lightly sclerotized, epistomal suture unsclerotized. Labral sclerite absent; clypeolabral area with lightly scerotized central region, lenticular in shape, with moderately sclerotized dorsal margin, bearing setae and two clypeolabral plates near its ventral margin. Stipital sclerite present and strongly sclerotized, more or less horizontal; cardo absent. Pleurostoma lightly sclerotized; posterior struts of inferior mandibular processes not connected by band; accessory pleurostomal area absent. Hypostoma long and strongly sclerotized, lateral end not divided in two at posterior tentorial pit and without extensions; accessory hypostomal area absent. Hypostomal spur present, about 1.5 × as long as its basal width. Labial sclerite nearly circular, moderately to strongly sclerotized. Salivary orifice U-shaped. Prelabial sclerite present as lightly sclerotized transverse band, connected to interior ventral margin of labial sclerite by weakly sclerotized projection of labial sclerite. Labial sclerite with six setae. Prelabial area with four setae. Maxillary and labial palpi each bearing two sensilla. Mandible strongly sclerotized; blade about 0.6 × as long as full mandibular length, without fine denticles. Antenna without papillus. Parietal band not visible. Spiracle with closing apparatus absent; intercalary trachea absent, subatrium about 2.0 × as long as atrium. Skin covered with small, bubble-like protuberances; spines absent; setae present, short and scattered.

Using the key to subfamilies in Short (1978), almost all the above characters would place *I. goesi* in Ctenopelmatinae. The one ambiguous feature is the sclerotized area on the clypeolabral surface. Short (1978) interprets this as the labral sclerite, recording it in the following ctenopelmatines: Euryproctini – *Euryproctus luteicornis* (Gravenhorst); Mesoleiini – *Protarchus testorius* (Thunberg); Perilissini – *Lathrolestes luteolator*, *Opheltes glaucopterus* (Linneaus), *Perilissus filicornis* (Gravenhorst) and *P. rufoniger* (Gravenhorst). He acknowledged this anomalous character for ctenopelmatines in a footnote but did not work it into his key. We were not able to examine Short's slides of these species but we did examine *Lathrolestes erythrocephalus* as part of this study. It too has the sclerotized clypeolabral feature (Fig. 28). However, the labral sclerites, as found in ectoparasitoid ichneumonids (Pimplinae, Xoridinae, Cryptinae,

Phygadeuontinae, Tryphoninae, etc.), are quite different from the sclerotized areas in *I. goesi* and *L. erythrocephalus.* Labral sclerites have well-defined borders and end with downturned 'knobs' that overlap the mandibles; the labral interior is not noticeably sclerotized. The structures in *I. goesi* and *L. erythrocephalus* have lateral ends that merge into clypeolabral plates, and have lightly to moderately sclerotized interiors. The structure is situated high on the clypeolabral area and does not overlap with the mandibles. Short (1978 figs 311–312) indicates something of this nature for his *Perilissus* species. The *Opheltes* example (Short 1978: fig. 316) is only a poorly defined arc. In summary, we do not believe that labral sclerites are present in the Ctenopelmatinae. Sharanowski et al. (2021) present a phylogenomic tree for the Ophioniformes. In the subfamilies beyond the Tryphoninae (which would best be called the 'higher Ophioniformes') the labral sclerite is absent in all known larvae, and we do not know of any reversals of this loss, notwithstanding Short (1978). The forthcoming study by Bernardo Santos and his collaborators (in prep.), using genomic ultraconserved elements (UCE), has sequenced some 500 genera of Ichneumonidae, though unfortunately not *Ischyrocnemis*. It would appear from their results that the sclerotized clypeolabral structure has arisen at least twice in ctenopelmatines: once in Perilissini and once in the rather distantly related *Euryproctus* (*Protarchus* was not sequenced).

Unsurprisingly, in view of its biology, the larva of *I. goesi* lacks the derived suite of characters found in Metopiinae, which all pupate within Lepidoptera pupae. The only subfamily into which *Ischyrocnemis* can reasonably be placed on larval grounds is the Ctenopelmatinae, which is entirely compatible with its developmental biology. However, its biological and larval characters are too generalized to fit easily into any of the recognized tribes.

Ctenopelmatinae sp. X
Figs 42, 43

This species was found only once, as a cocoon with a dead prepupa in a winter host cocoon resulting from an *Aprosthema* larva collected at Site 2. The unbanded light brown cocoon (Fig. 42) has a felted appearance quite different from cocoons of the other parasitoids encountered.

Final instar larval cephalic sclerites (Fig. 43). ***Specimen examined*****:** DBW 21.vi.2020a (NMS).

Cephalic structures generally moderately to strongly sclerotized. Epistoma lightly to moderately sclerotized; epistomal band present; dorsal margins of both poorly defined and merging with general light sclerotization of frons. Labral sclerite absent; clypeolabral area with weakly sclerotized central region, poorly defined crescentic band present; clypeolabral plates absent. Stipital sclerite present and strongly sclerotized, more or less horizontal; cardo absent. Pleurostoma lightly sclerotized; posterior struts of inferior mandibular processes not connected by band; accessory pleurostomal area absent. Hypostoma long and strongly sclerotized, lateral end not divided in two at posterior tentorial pit and without extensions; accessory hypostomal area partially present

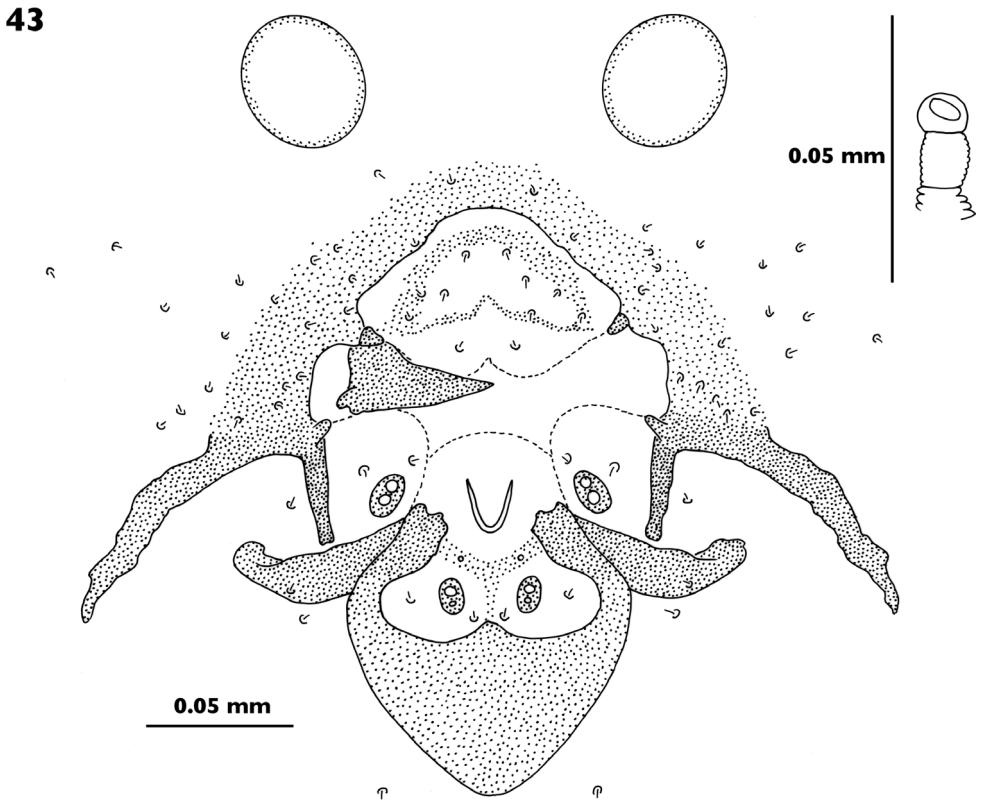


Figure 43. Ctenopelmatinae sp. X. Cephalic sclerites of final instar larva.

and lightly sclerotized. Hypostomal spur present, about 3.8 × as long as its basal width. Labial sclerite ovoid, ventral portion 0.6 × as long as length of labial sclerite, lightly to strongly sclerotized. Salivary orifice U-shaped. Prelabial sclerite present as weakly sclerotized transverse band, connected to interior ventral margin of labial sclerite by weakly sclerotized projection of labial sclerite. Labial sclerite with six setae. Prelabial area with four setae. Maxillary and labial palpi each bearing two sensilla. Mandible strongly sclerotized; blade about 0.6 × as long as full mandibular length, without fine denticles. Antenna without papillus. Parietal band present as lightly to moderately sclerotized vertical oblong with irregular margins. Spiracle with closing apparatus absent; intercalary trachea absent, subatrium about 1.5 × as long as atrium. Skin covered with small, bubble-like protuberances; spines absent; setae present, short and scattered.

This specimen can be unequivocally placed to Ichneumonidae using the keys and illustrations in Short (1952), Čapek (1970, 1973), and Finlayson (1987). As with *Ischyrocnemis goesi*, this specimen runs to Ctenopelmatinae in Short (1978) but cannot be placed further. Short used tribes based on adult characters and then created keys based upon character combinations that appear to be useless. While some ctenopelmatine genera or groups of genera seem distinct, no match is evident for Ctenopelmatinae sp. X.

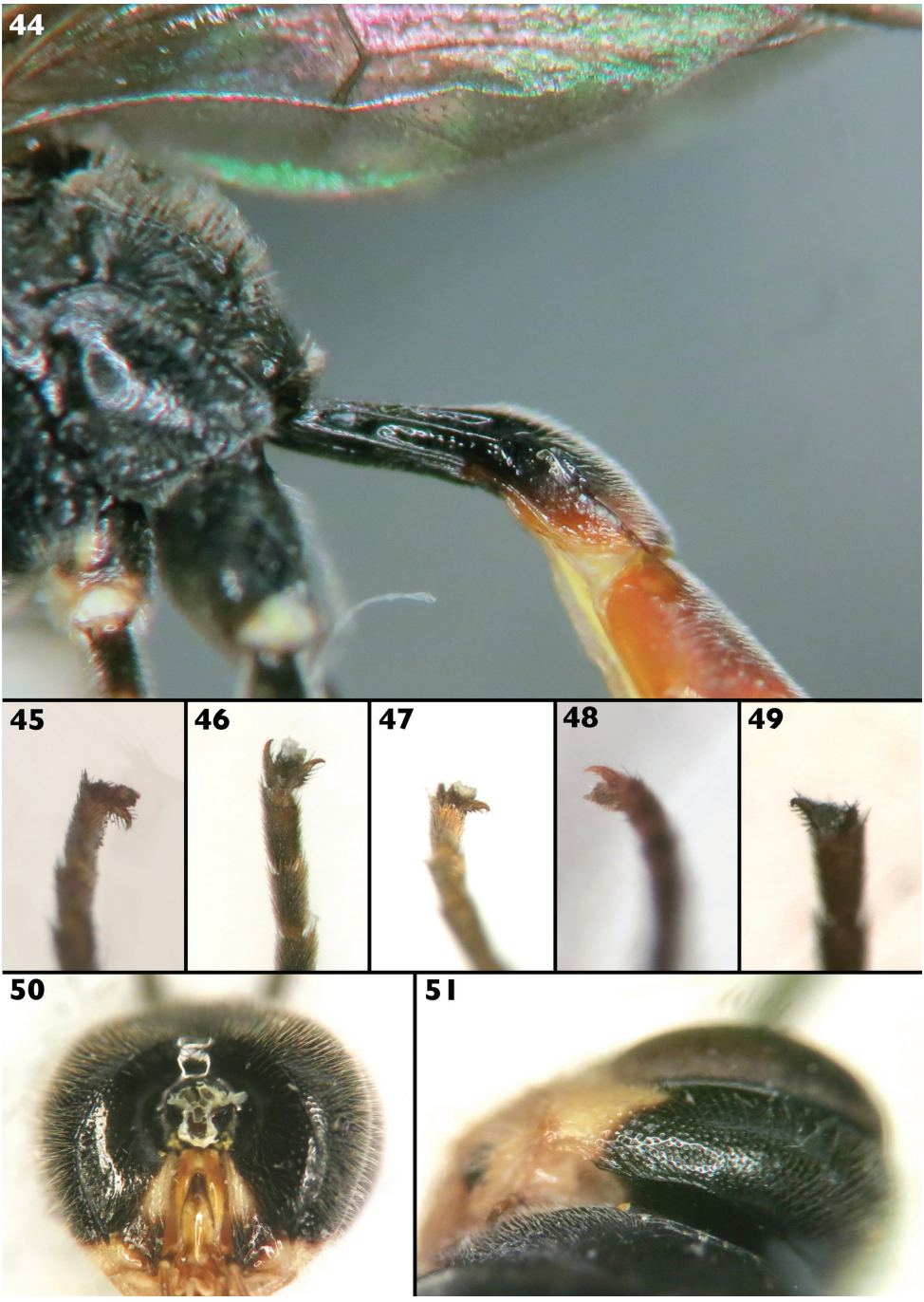
***Terozoa quadridens* (Tryphoninae, Tryphonini)**
Figs 44–47, 50–68; FilmingVarWild videos 5–7, 13

Taxonomy. *Terozoa* is a Eurasian genus of only three or four species that are taxonomically ill-understood. Nothing is published on the biology of any species. The taxonomic history of *Terozoa* is complex. The genus was first described (Förster 1869) without an included species, but one was designated by Perkins (1962) by the description of the single specimen standing as *Terozoa* in Förster's collection, a male, as *Terozoa quadridens* Perkins, 1962. That remained a little-known and poorly understood species, and Townes (1971) erroneously treated *Terozoa* as a junior synonym of the genus *Ischyrocnemis* Holmgren, 1858 (type species *Iscyrocnemis goesi* Holmgren, 1858), that Townes (1971) placed, but only tentatively, in the subfamily Metopiinae. At that time both nominal genera each contained a single species, and nothing was known of their biology. Townes's (1971) mistaken synonymy led to Scaramozzono (1995: 56) incorrectly placing *Ischyrocnemis* in Tryphoninae following his detection of an externally-borne egg on the ovipositor of a specimen he recognised as "*Ischyrocnemis*" *quadridens*; ironically confounding the credit due to him of first recognising *Terozoa* as a tryphonine. Perkins (1962) had in fact previously recognised them as distinct genera, but placed both in Ctenopelmatinae.

Soon after Townes's generic classification, an unusual genus of Tryphoninae, *Parablastus* Constantineanu, 1973, monobasic with type species *Parablastus bituberculatus* Constantineanu, 1973, was described and placed in Tryphonini, again with nothing known of its biology. Bennett (2015) included *Parablastus* in his generic treatment of Tryphoninae but, as he had not seen a specimen, and because the original description was not particularly rich in detail, the genus does not run smoothly in Bennett's (2015) key, largely because at least some species have an apparent glymma (Fig. 44, but see below).

Kasparyan (2019a), in a paper treating both *Terozoa* and *Ischyrocnemis* at species level, resurrected *Terozoa* from the synonymy of *Ischyrocnemis*, recognised *Terozoa* as a genus of Tryphonini, and placed *Parablastus* as a junior synonym of it. Because three nominal species had been described in *Parablastus*, new combinations were established for *Terozoa bituberculata* (which he synonymised with *Terozoa quadridens*, but see below), *T. iberica* (Kasparyan, 1999) and *T. anatolica* (Gürbüz & Kolarov, 2005). No species that would now be classified as *Terozoa* has previously been recorded from France.

The identification of *Terozoa* species is bedevilled by firstly quite profound and unusual sexual dimorphism (except for *T. iberica*, males have predominantly or entirely black faces while in females the face is largely yellow), and secondly the fact that descriptions of new species have not been supported by examination of types of species already described, and some characters have been misinterpreted or expressed in vague terms. Thus keys, which have not been based on examination of specimens believed to represent all species, have perpetuated earlier mistakes. Through the kindness of Stefan Schmidt (ZSM) we have been able to borrow the holotypes of both *T. quadridens* (a male, in fairly good but not perfect condition) and the nominal *Parablastus anatolicus*,



Figures 44–51. *Terozoa* species **44–47, 50, 51** *T. quadridens* **48, 49** *T. anatolica* **44** first metasomal tergite (female) **45–49** inner hind claws **45** male (holotype) **46** male (reared) **47** female **48** male **49** female **50** posterior of head (female) **51** lower gena (female).

Figures 52–53. *Terozoa quadridens* female **52** in life **53** mounted.

a female which was accompanied by a clearly conspecific male paratype (both in good condition). The pair of *T. anatolica* has been crucial for understanding aspects of sexual dimorphism in the genus. Unfortunately our attempt to borrow (or to obtain photographs of) the female holotype of the nominal *Parablastus bituberculatus* from the Constantineanu collection was unsuccessful, but photographs of the female holotype and male paratype of *T. iberica* have been examined.

The determination of our species was problematical because for most of the duration of the project we had only females (N = 6). In 2021, however, we succeeded in rearing a male specimen, which agrees well with the type of *T. quadridens*, the main difference being its entirely black first metasomal tergite (postpetiole becoming brownish in holotype of *T. quadridens*, as indeed is the case for all other species except for *T. ibericus* in which T1 is more extensively yellowish posteriorly (Kasparyan 2019a)). We had already concluded that our females are not *T. bituberculata*, as they all have a completely black propodeum, and claws strongly pectinate basally, unlike the original description (Constantineanu 1973) of the female of *T. bitubercuata* which indicates orange markings on the propodeum and claws with only a comb of setae. Contantineanu (1973) makes no mention of a glymma, but whether or not this is because it is lacking in *T. bituberculata* is unclear. Through examination of the female holotype we also ruled out *T. anatolica*, which is a shorter/broader insect than our material, the female holotype having a noticeably shorter mesosoma and broader metasomal tergites (T2 0.9 and T3 0.7 × as long as wide, as against respectively 1.2–1.3 and 0.8–1.0 in our females), weaker pectination of claws and interstitial 1cu-a in the fore wing (postfurcal in the type of *T. quadridens* and in all the specimens resulting from our field-work, though in one female nearly interstitial). Also the male of *T. anatolica* has yellow marks at the upper corners of the clypeus and in the lower part of the inner orbits and malar space (face completely black in male *T. quadridens*; only the clypeus with a yellow band, which is also present but nearly broken centrally in the male paratype of *T. anatolica*). The Transcaucasian *T. iberica*, which is much more richly yellowish marked, as illustrated by Kasparyan (2019a), can also be excluded. Accepting our species as *T. quadridens* refutes Kasparyan's (2019a) synonymization of *T. bituberculata*, which was based largely on his assumption that there would be only one species in

the relatively well-studied strictly European fauna (Dmitri Kasparyan, pers. comm.), and we here resurrect *T. bituberculata* (Constanineanu, 1973) (stat. rev.).

The difference in body colour between the two sexes of *T. quadridens* from our study are as follows. Male: head black except apical band on clypeus and small mark adjoining vertical orbit yellow (mandible subapically and palpi in part yellowish); mesosoma entirely black. Female: Head black except the following yellow: face almost entirely (except for a small area ventral of antennal socket between it and yellow inner orbit) and clypeus, vertical mark in orbit, malar area and genae to above the lower level of eye, mandible except blackish teeth, and palpi (partly); mesosoma black but with propleuron (in one specimen diffusing into pronotal collar), subalar prominence, posterior band on scutellum, band on metanotum (sometimes nearly divided into two spots) yellow.

Genbank accession numbers for *T. quadridens* from our study (SK_19_48): CO1 OK393910; 28S OK393940.

While it is our view that more material is needed to inform the taxonomy of European and Anatolian species of *Terozoa*, to make the most of our opportunity to examine some relevant specimens we give a brief provisional key to species below, and then comment on some characters that have previously been used to separate species that appear to have little value, or have been misstated:

Provisional key to the species of *Terozoa* Förster

Note: The characters for *T. bituberculata* are from the original description, and the male is unknown.

1 Pronotum completely yellow. Head of female predominantly yellow. Face of male yellow ..... ***T. iberica* (Kasparyan)**

– Pronotum predominantly black. Head of female (except for face) predominantly black. Face of male (if known) predominantly black **2**

2(1) Propodeum of female black with two yellow spots. Hind tarsal claws of female with setal comb but without clear teeth ..... ***T. bituberculata* (Constantineanu), stat. rev.**

– Propodeum of female completely black. Hind tarsal claws of female pectinate at base (Figs 47, 49) **3**

3(2) Female with metasomal T2 1.2–1.3 × and T3 0.8–1.0 × as long as wide. Male with face completely black ..... ***T. quadridens* Perkins**

– Female with T2 0.9 × and T3 0.7 × as long as wide. Male face black with yellow in ventral orbits and malar space ..... ***T. anatolica* (Gürbüz & Kolarov)**

Comments on characters used elsewhere

(i) Posterior carination of area superomedia of propodeum. Kasparyan (2019a) includes a key in English in which it is mistakenly said that the area superomedia is open in *T. anatolica* (despite fig. 6 in Gürbüz and Kolarov 2005). In fact, the area

superomedia is closed by a distinct carina in both examined specimens of *T. anatolica*, and also in both examined males of *T. quadridens*, but in our females of *T. quadridens* it varies from being closed by a well-defined carina to, in other specimens, being marked posteriorly only by the first of a series of transverse ridges of about equal strength that are present in the anterior half of the area petiolaris (thus arguably presenting as open). The posterior carina of the area superomedia is incomplete medially in (at least) one female paratype of *T. iberica* (Andrew Bennett, pers. comm.), and Constantineanu (1973) states that it is open posteriorly in *T. bituberculata*.

(ii) Interception of nervellus. This is very close to the middle in all specimens examined, only marginally but perhaps significantly above the middle in both specimens of *T. anatolica*.

(iii) Pectination of claws. Despite Perkins's (1962) assertion of simple claws, the holotype of *T. quadridens* has what amounts to weak pectination in the basal part of the hind claws (Fig. 45) although it can be hard to appreciate as being more than just setiform along the length of the claw, the aged specimen being somewhat grimy. In the male reared during the present work similar rather weak pectination is clearly discernible (Fig. 46), while in all of the females it is much stronger (Fig. 47), though seemingly rather variable. The apparent range in the females is at least equal to the negligible difference between the two males. In *T. anatolica* the claws are apparently weakly setose in the male (Fig. 48) with weak pectination clearer in the female (Fig. 49) (in the original description the pectination is greatly over-drawn: Gürbüz and Kolarov 2005: fig. 5). The claws of female *T. iberica* are strongly pectinate to beyond the middle (Andrew Bennett, pers. comm). In the original description (Constantineanu 1973) the explicitly stated absence of teeth (in the generic diagnosis of *Parablastus*), followed by the rather different expression of setiform claws in the female of the nominal *P. bituberculatus*, should be checked if the holotype ever becomes available for examination.

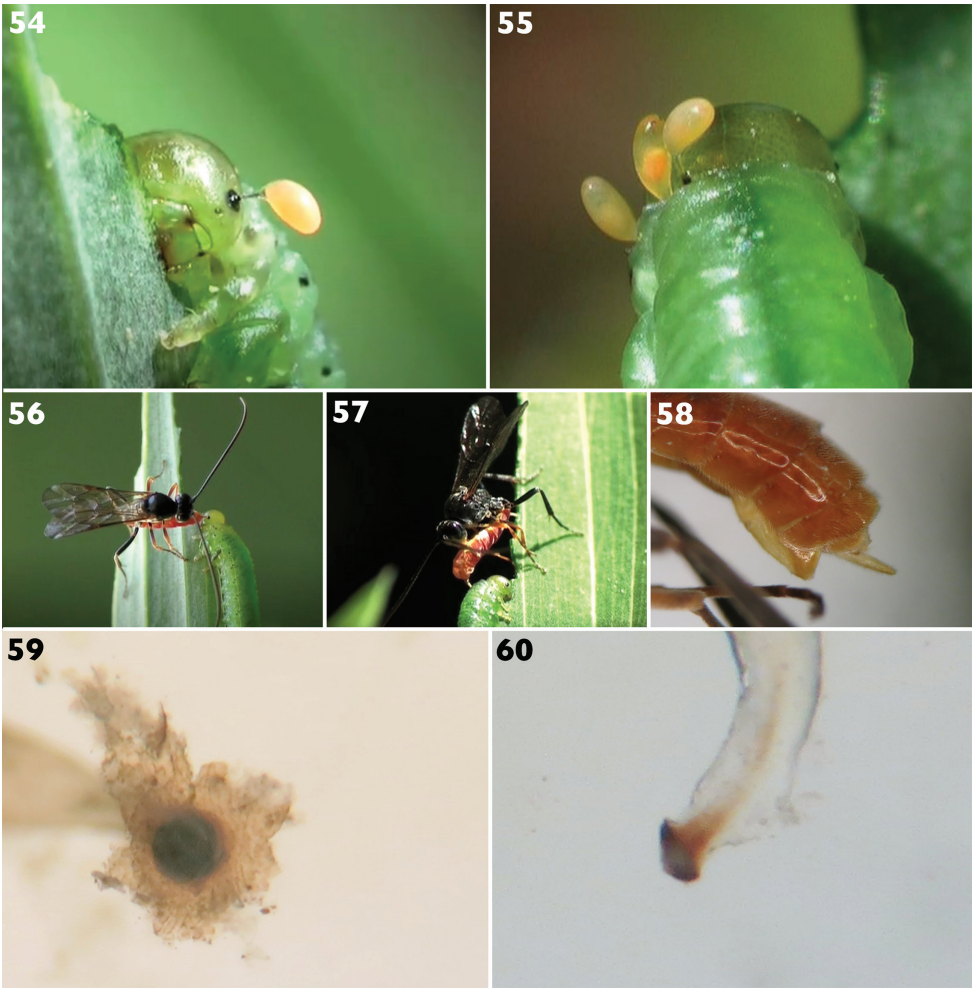
(iv) Number of antennal flagellomeres. The antennae of the type of *T. quadridens* are broken. The female type of *T. anatolica* has 43 and the male paratype has 42. The female type of *T. bituberculata* was said to have 44, and *T. iberica* was described as having 33–39. Our series of females of *T. quadridens* have 44–48 flagellar segments, but our male only 40 (progeny of a female with 45). Although differences in the number of flagellomeres has been used to separate species, the large range seen in our series of *T. quadridens* suggests that the character should be used with caution.

(v) Junction of hypostomal and genal carina. There is no hypostomal carina *per se* discernible in any of the specimens of *T. quadridens* and *T. anatolica* examined, but there is a series of two or three weak ridges developing on the lower occiput that run into the occipital carina well before the mandible and reinforce it as a weak expansion (a short tooth-like crest) near the junction of the two colours of the gena (Figs 50, 51). The strength of the crest (but less so its position) varies a little between the specimens seen, including within our series of female *T. quadridens*. The hypostomal carina is apparently lacking also in *T. iberica* (Andrew Bennett, pers. comm.) despite mention of it by Kasparyan and Tolkanitz (1999), and it goes unmentioned in the original description of *T. bituberculata*.

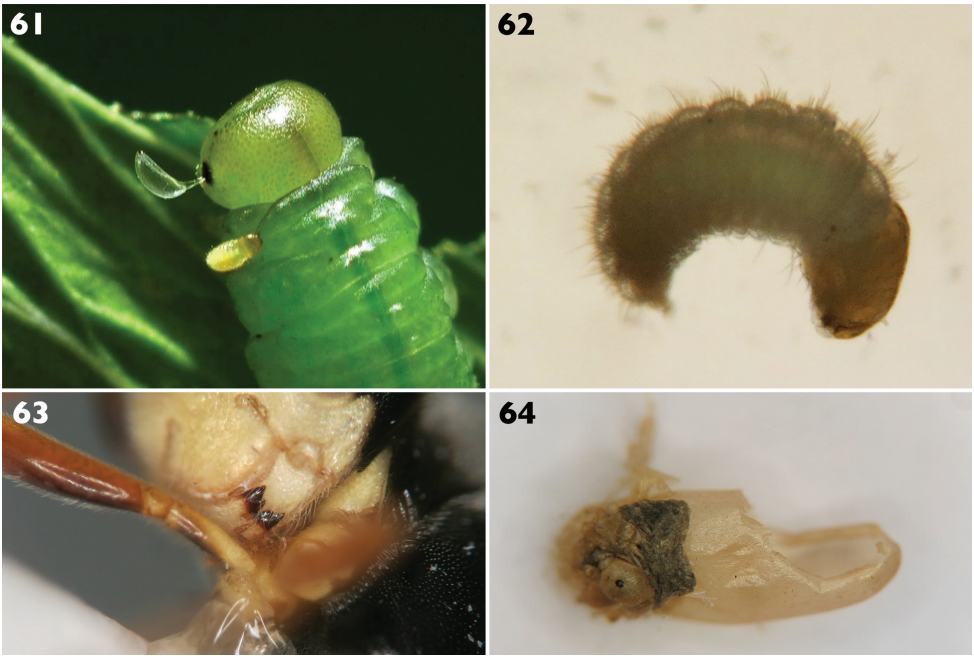
(vi) Presence or absence of a glymma. Confusion may have arisen in judging whether a glymma is present or not. Perkins (1962) mentions a deep glymma in the holotype of *T. quadridens*, and the identical structure is seen in all our specimens of this species (Fig. 44). The structure comprises a rather deep and wide trough between the dorso-lateral carina and the ventro-lateral carina of metasomal tergite I that is roughly parallel for the length of the petiole, with a further depression in the extreme anterior part. A comparable structure, but with a slightly less deep anterior depression, is also present in the holotype of *T. anatolica*, although the structure is not mentioned (let alone referred to as a glymma) in the original description. Constantineanu's (1973) description of the monotypic genus *Parablastus* and included nominal species *P. bituberculatus* does not mention a glymma and the generic diagnosis (of *Parablastus*) presented by Kasparyan and Tolkanitz (1999) explicitly states it to be absent, from which Bennett (2015) concluded that there is no glymma. It is unclear whether or not the structure deemed by Perkins (1962) to be a glymma is moderately uniform within the genus, nor whether it should properly be regarded as a glymma homologous with the condition in various other Tryphonini.

Biology. *Terozoa quadridens* (Figs 52, 53) was the second most abundant parasitoid found in the study, present at all four sites in Var (Table 2). Females were regularly seen searching (six were collected), and final instar host larvae bearing pinkish orange eggs (Figs 54, 55) were also often found. It is apparently univoltine and occurs late in the host's season overall, being absent from its early generations. The host is attacked only in its final instar, and the female wasps have been observed to monitor penultimate instar hosts, returning frequently over several days, finally to parasitise them once they have moulted. The parasitoid patiently stalks the final instar host, sometimes over a long period (up to 90 mins has been observed), during which the host usually continues to feed unperturbed – even as the egg is laid. For this, the parasitoid's metasoma is flexed under the mesosoma to project in front of the face, allowing for visual control of the precise egg placement (Figs 56, 57). No antennation or other contact is made with the host before the moment of insertion of the ovipositior. Once that happens it still takes several seconds before the egg is actually deposited. Unusually for a Tryphonini (in the restricted sense of Kasparyan 2019b), the egg is not seen carried below the shaft of the ovipositor before being laid, but rather it is concealed by the large hypopygium (Fig. 58) almost until deposition; indeed it is not certain that it doesn't remain at least partly in the oviduct until needed. The body of the egg is faintly reticulate and ca 0.6 × 0.2 mm, with a translucent and gradually narrowing stalk ca 0.2 mm long (Fig. 54). Most eggs are laid on the head of the host, very frequently in its eye (stemma) (Fig. 54), and less commonly on the first thoracic segment (Fig. 55). When an ovipositing female targets the eye she is unwavering in that aim throughout the stalking process, however long it takes, and no case of failure to fulfil the intention has been seen. The anchor of the egg is unfortunately difficult to assess from material to hand as, even after maceration with KOH, the egg does not detach easily from host tissue (and it was decided not to sacrifice one of our few adult specimens in order to examine the ovarian egg), but the anchor appears to be very small, about 0.05 mm

across, and stud-like (Figs 59, 60). The substantial period immediately prior to actual oviposition, during which the ovipositor is held in position having pierced the host's integument, might indicate that some kind of cementing rather than just a physical anchor is involved. Superparasitism is frequent: self-superparasitism during closely-spaced visits has been observed, but several hosts have been found with eggs apparently in different states of embryonic development (Fig. 55), suggesting that already-parasitised hosts are oviposited on rather than being rejected, and this seems to be the main source of superparasitism. Of 31 host larvae found in the field with *T. quadridens* eggs, 15 carried one egg, 12 two eggs, two three eggs, and one each had four and five eggs. Egg positions are generally more dorsal than lateral. No host-feeding was seen, either in the field or in captivity.



Figures 54–60. *Terozoa quadridens* **54, 55** egg(s) on host **56, 57** oviposition stance **58** apex of female metasoma **59, 60** egg attachment **59** from below (through host cuticle) **60** after maceration.



Figures 61–64. *Terozoa quadridens* **61** hatched egg in eye of host with first instar larva on its thorax **62** first instar larva **63** adult mandible **64** cocoon.

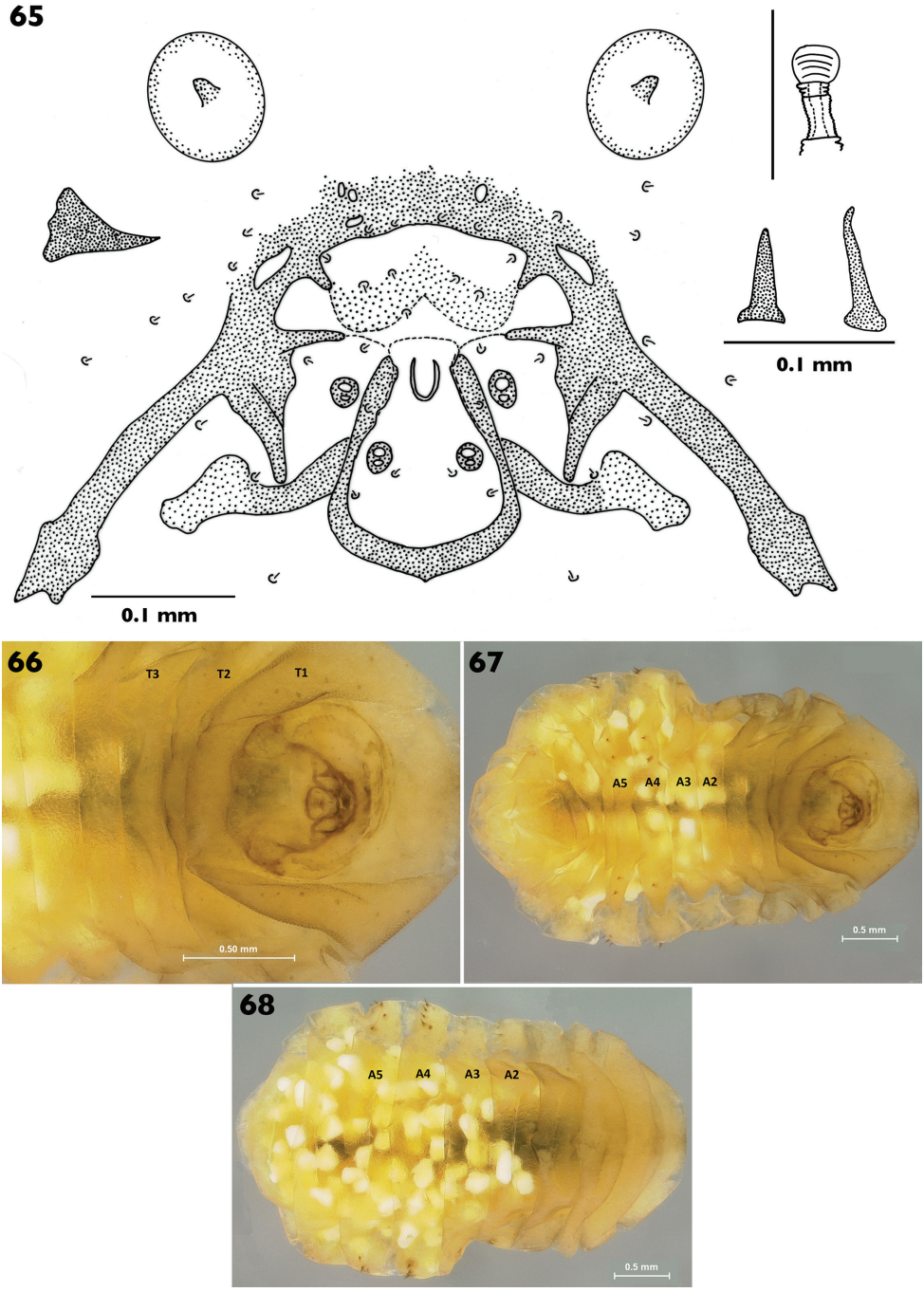
Normally the host forms its cocoon about four days after entering its final instar and the *T. quadridens* egg hatches also after about four days, by which time the host is usually cocooned. Possibly due to captive conditions, on three occasions an egg hatched on a still-exposed host, and the first instar larva was seen to leave its eggshell entirely and move from the host's presumably impenetrably hard head capsule to commence feeding on a thoracic segment (Fig. 61); however, these first instar larvae (Fig. 62), having completely left their anchored eggshell, were easily dislodged and lost without the security of the host cocoon. Of host larvae parasitised by *T. quadridens* that survived to make cocoons, 20 made winter cocoons and five made summer cocoons, showing that forming a winter cocoon by the host is not caused by any action of *T. quadridens*. From two of the summer cocoons a female *A. tardum* subsequently emerged, in one case slightly deformed (lacking one antenna). These are important rearings, as they demonstrate that *T. quadridens* requires a diapausing host to have a chance of success, presumably because the parasitoid cannot develop rapidly enough to overwhelm a summer-developing host. As well as correlating with the adult's quadridentate mandibles (Fig. 63), this need helps to explain why it flies relatively late in the season, when the overwhelming majority of hosts will make winter cocoons, and it may also account for our great difficulty in rearing a specimen, the usual outcome from winter cocoons of hosts parasitized by *T. quadridens* being either a host prepupal death with the *T. quadridens* larva scarcely developed, more rarely an adult *A. tardum*

the following spring, or in several cases a *T. quadridens* cocoon containing a dead prepupa. The pale yellow-brown unbanded cocoon (Fig. 64) is constructed within that of the host; several cocoons have been obtained from hosts making winter cocoons, but the *T. quadridens* has not developed to adulthood except in just one case when a male emerged on 16.v.2021, the host having been killed as a prepupa. This specimen was from one of six definite *A. tardum* (ab ovum) parasitised in captivity (with one egg) on 25.v.2020. However, we noted that some *T. quadridens* cocoons that were still unemerged more than a year after formation contained soft (though dead) prepupae, that suggests an ability to enter prolonged prepupal diapause, as has been noted in several Tryphoninae (Bennett 2015, and references therein).

Adults of both *I. goesi* (once) and *L. erythrocephalus* (several times) were reared from hosts bearing *T. quadridens* eggs, undoubtedly owing to the faster feeding of these ctenopelmatines once the host became a prepupa.

Final instar larva and cephalic sclerites (Figs 65–68). ***Specimens examined*****:** DBW 21.vi.2020b, 21.vi.2020c, 21.vi.2020d, 21.vi.2020e (all NMS).

Cephalic structures (Figs 65, 66) generally moderately to strongly sclerotized. Epistoma strongly sclerotized; epistomal band present with several small openings; dorsal margins of both poorly defined and merging with general light sclerotization of frons. Labral sclerite absent; clypeolabral area with two low convex lobes, ventral 0.5 of lobes lightly to moderately sclerotized, bearing setae and without clypeolabral plates. Stipital sclerite present and strongly sclerotized, more or less horizontal; cardo absent. Pleurostoma strongly sclerotized and with two large lateral openings; anterior strut of inferior mandibular process elongate (posterior struts not connected by band); accessory pleurostomal area absent. Hypostoma long and strongly sclerotized, lateral end not divided in two at posterior tentorial pit and without extensions; accessory hypostomal area absent. Hypostomal spur present, about 1.7 × as long as its basal width. Labial sclerite quadrate, strongly sclerotized. Salivary orifice U-shaped. Prelabial sclerite present as lightly to moderately sclerotized triangle without definite borders. Labial sclerite with 6 setae. Prelabial area with 4 setae. Maxillary and labial palpi each bearing two sensilla. Mandible strongly sclerotized; blade 0.6–0.7 × as long as full mandibular length, not bifurcated, denticles absent. Antenna papillate. Parietal band present as lightly to moderately sclerotized vertical oblong with irregular margins. Spiracle with closing apparatus present; intercalary trachea present, subatrium about 0.9 × as long as atrium. Skin (Fig. 66) covered with small, bubble-like protuberances; setae generally few, small (20–30 μ) and concentrated on thoracic segments 1–2 (Fig. 66), but abdominal segments 1–4 each with two clusters of longer, spine-like setae (Figs 67, 68): abdominal segments 1–2 with moderately sclerotized elongate, cone-like setae with apices often gently curved, 70–80 μ in length, clusters located on lateral dorsal and ventral surfaces; abdominal segments 3–4 with strongly sclerotized cone-like setae (stouter than on abdominal segments 1–2), 50–60 μ in length, clustered as on abdominal segments 1–2. Length of spine-like abdominal setae ≥ length of mandibular blade. (The ventral pair of prelabial setae could not be figured owing to their position).



Figures 65–68. *Terozoa quadridens*, final instar larva **65** cephalic sclerites **66–68** dried up (prepupa) **66, 67** ventral **68** dorsal.

Short's (1978) belief that all tryphonine larvae possessed a labral sclerite has been dominant (Bennett 2015). In particular, Short wrote that the *Exenterus* Group of Tryphonini (Cteniscini *sensu* Short) had the dorsal margin of the labral sclerite fused with the epistomal band. Gupta (1990) pointed out that *Erromenus* Holmgren had this character as well, and Bennett (2015) noted the same for *Boethus* Förster: both genera belong to genus-groups other than the *Exenterus* Group. Therefore we were greatly surprised to discover that both *Terozoa quadridens* and *Thibetoides aprosthemae* lacked any trace of the labral sclerite. In fact Short (1978: 36) did mention that Finlayson (1960a) treated *Exenterus* as lacking the labral sclerite, although he did not accept her interpretation. We therefore: (i) re-examined Short's slides of *Exenterus* species (*abruptorius* (Thunberg), *adspersus* Hartig, *amictorius* (Panzer), *nigrifrons* Rohwer, *tricolor* Roman) in NMNH, and (ii) made fresh slides of *Excavarus* spp. (*etrocaulus* (Mason) and *rufipes* (Uchida)) and *Exenterus* species (*abruptorius*, *adspersus*, *amictorius*, and *tricolor*) from EMUS. During the process of slide preparation, four of the species (*etrocaulus*, *rufipes*, *amictorius*, *tricolor*) were examined at 50× with a dissection microscope: the region of the epistomal band and clypeolabral area could be clearly seen in three-dimensions and in no instance was a labral sclerite observed. The epistomal band is rather thick and can flex after mounting, presenting the ventral margin: this thick ventral margin is prominent and is probably what Short (1978) interpreted as a fusion of the epistomal band and dorsal margin of the labral sclerite. Concerning the ventro-lateral arms of the supposed labral sclerite that he and Bennett (2015) drew, the clypeolabral area in the best-preserved specimens appears to be convex, or bilaterally convex, and the pressure of the cover slip distorts this region, pushing the ventral margin down over the mandibles. It appears that either the ventral margin is lightly sclerotized or is thickened and distorted by the mounting pressure. In either case, the ventral clypeolabral margin can be imagined to be part of the labral sclerite to the willing eye. Bennett (2015) was more tentative in his illustrations and drew them as thin lines, whereas Short drew them more positively as definite thickened sclerites – which are definitely not present in his source slides. Thus we believe that all of the *Exenterus* Group lack the labral sclerite – as do the other tryphonini genera reported to have fusion of the epistomal band and labral sclerite. Looking at the tryphonine generic cladogram in Bennett (2015: fig. 7b), it appears that loss of the labral sclerite has occurred on several occasions, although it would be premature to speculate, especially since ongoing phylogenomic research on generic relationships is causing some changes (Andrew Bennett, pers. comm.). Finally, most tryphonine genera have elongate setae; although *Tryphon* species have them quite stout and almost peg-like (Short 1978). Their exact disposition on the body has not been previously known. *Terozoa quadridens* has large conical setae of types not previously seen; a dried prepupa has provided details of distribution (Figs 67, 68).

***Thibetoides aprosthemae* Shaw, 2018 (Tryphoninae, Tryphonini)**
Figs 69–78; FilmingVarWild videos 8–11

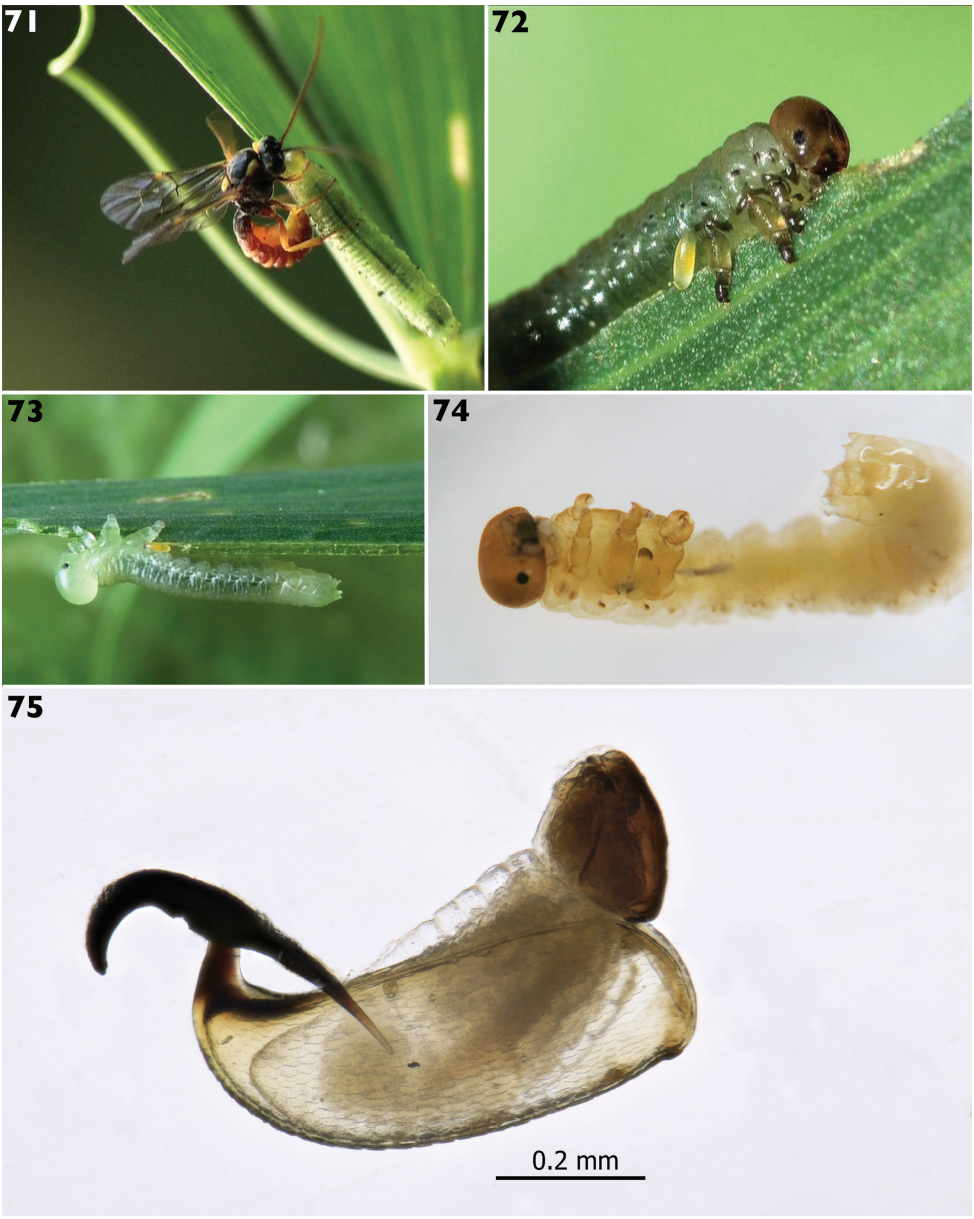
Taxonomy. *Thibetoides* Davis, 1897 is a small Holarctic genus (one N. American and three or four Palaearctic species) with the unusual character within Tryphoninae of having the first and second metasomal tergites immovably fused, and it is distinguished from

Figures 69, 70. *Thibetoides aprosthemae* female **69** in life **70** mounted.

the related Afrotropical genus *Ibornia* Seyrig by furthermore bearing a horn in the supra-antennal area (vertical lamella present on frons in *Ibornia*) (Bennett 2015). The specimen that was to become the holotype of *Thibetoides aprosthemae* was reared on 29.v.2014 from a summer cocoon collected on 11.v.2014 that was later identified as having been made by *A. tardum* (Shaw et al. 2018) and accordingly recorded from France, and this chance discovery was the stimulus for the present study. Otherwise *T. aprosthemae* was found only in 2019, but then in three of the four Var sites and also at Apricale (Table 2). The further specimens thereby reared are so varied in colour (Figs 69, 70), which to a large extent has been used to distinguish between the Palaearctic species, that a review of the taxonomy of Palaearctic species may be desirable. That is beyond the scope of the present work and all four of the specimens reared in this study are presumed to belong to *T. aprosthemae*, in whatever way that nominal taxon may come to be interpreted in the future.

Genbank accession numbers of *T. aprosthemae* from our study (SK_19_47): CO1 OK393911; 28S OK393939.

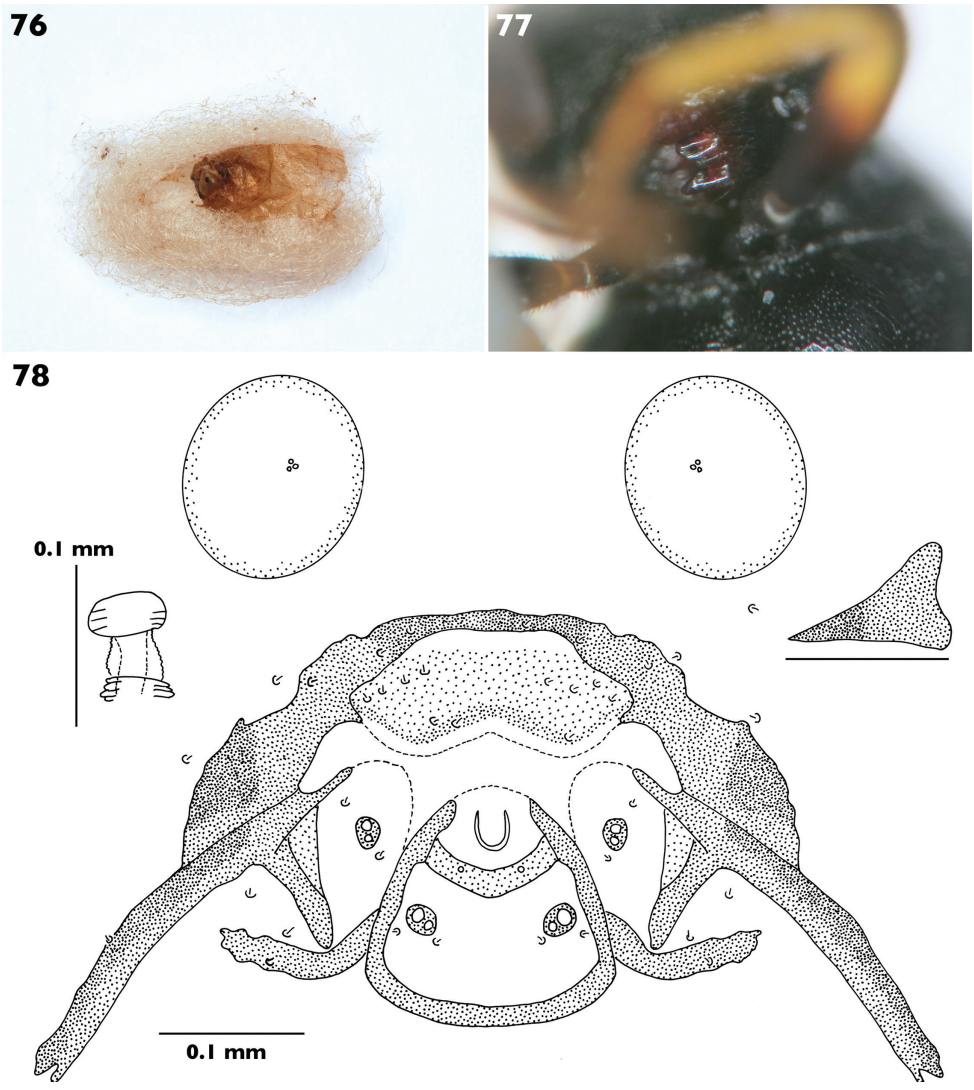
Biology. Despite our rearing only four specimens overall, and not seeing adults at large in the field, *Thibetoides aprosthemae* (Figs 69, 70) was found to occur at three of the Var sites and was also detected from its egg, but not reared, at Apricale in Italy (Table 2). However it was scarce, only seven host larvae parasitised by *T. aprosthemae* being found. It is clearly plurivoltine, and both in captive experiments (Fig. 71) and in the wild the 0.7 × 0.2 mm yellow egg (Figs 72, 73) was found to be laid, singly, behind the third thoracic leg (several observations of this precise placement) except for one oviposition (on a slightly older and hence longer host) behind the second thoracic leg (Fig. 74). The hosts could be as small as 4 mm in length (2nd instar). During the oviposition process on 2nd and early 3rd instar hosts the antennae seem to be used mainly to assess the state of the leaf edge, only briefly the host, before the female parasitoid walks along the unreactive host, orientating more or less head-to-head and holding it with all legs during the approximately 5–7 seconds it takes to oviposit. Larger hosts (8–9 mm; presumed to be late 3rd instar) were offered but they defended themselves and were not always parasitised efficiently, the parasitoid egg sometimes ending up on the host's side or dorsum where it failed to develop (the oviposition process also tended to take longer; up to 12



Figures 71–75. *Thibetoides aprosthemae* **71** ovipositing **72, 73** egg on host **72** on 2nd instar host **73** host just moulted with egg still intact **74, 75** first instar larva protruding from egg **74** on dead host **75** dissection revealing egg anchor.

seconds). Although during skirmishes, especially with later instar hosts, there was more contact, hosts did not appear to be subdued by being stung. The parasitised hosts are able to moult both successfully and repeatedly without dislodging the deeply anchored egg (Figs 73, 75). After about 7 days the egg hatches, but the larva remains partly within the eggshell (Figs 74, 75) during the growth of the host larva (which almost conceals

the parasitoid) and does not progress beyond the first instar before the host has formed its cocoon. Host moulting failures (leading to death, Fig. 74) sometimes occurred, but were usually attributable to the host's also being parasitised by *L. erythrocephalus*, as evidenced by its black eggshell and sometimes a moving larva visible in the host's body. We reared *T. aprosthemae* from summer cocoons (emerging end of May and end of June) and also from a winter cocoon in which the parasitoid had overwintered (emerging mid-April), giving a good indication that it can have (at least) three annual generations. The unbanded rather frail yellowish cocoon (Fig. 76) is formed within that of the host. The adult mandible has its upper tooth slightly divided (Fig. 77).



Figures 76–78. *Thibetoides aprosthemae* **76** cocoon with host remains, partly removed from host cocoon **77** adult mandible **78** cephalic sclerites of final instar larva.

Although hosts multiparasitised by *T. aprosthemae* and *L. erythrocephalus* often die through failing to moult successfully into their fourth instar (three observations in the field), we have also reared *L. erythrocephalus* from that situation.

Final instar larval cephalic sclerites (Fig. 78). ***Specimen examined*****:** DBW 14.vi.2020b (NMS).

Cephalic structures generally moderately to strongly sclerotized. Epistoma moderately to strongly sclerotized; epistomal band present. Labral sclerite absent; clypeolabral area with lightly sclerotized central region, bearing setae and without clypeolabral plates, ventral margin of clypeolabral area moderately sclerotized; clypeolabral area appears to be bilaterally convex. Stipital sclerite present and strongly sclerotized, more or less horizontal; cardo absent. Pleurostoma moderately sclerotized; anterior struts of inferior mandibular processes elongated, posterior struts of inferior mandibular processes not connected by band; accessory pleurostomal area present. Hypostoma long and strongly sclerotized, lateral end weakly divided in two at posterior tentorial pit and without extensions; accessory hypostomal area absent. Hypostomal spur present, about 1.5 × as long as its basal width. Labial sclerite quadrate, moderately to strongly sclerotized. Salivary orifice U-shaped. Prelabial sclerite indicated by lightly sclerotized transverse area. Labial sclerite with 6 setae. Prelabial area with 4 setae (uncertain owing to distortion). Maxillary and labial palpi each bearing two sensilla. Mandible strongly sclerotized; blade about 0.6 × as long as full mandibular length, not bifurcated, presence/absence of denticles unknown. Antenna disk-like, with several sensilla in place of papillus. Parietal band present as lightly to moderately sclerotized vertical oblong with irregular margins. Spiracle with closing apparatus present; intercalary trachea absent, length of subatrium about equal to that of atrium. Skin covered with small, bubble-like protuberances; setae generally few, small, and widely scattered but with a few scattered long setae present, 20–30 μ in length and length < length of mandibular blade (position on abdomen cannot be determined).

The number of prelabial setae is unclear, as the prelabial area is torn and folded up and over the ventral portion of the labial sclerite – the exact positioning of the setae cannot be ascertained. The mandibles are oriented with the outer surface toward the observer and so the inner part of the blade cannot be examined for the presence or absence of denticles.

The most notable features are: (i) the absence of the labral sclerite, discussed in detail in the section on *Terozoa quadridens*, and (ii) the spiracular morphology. Almost all known tryphonine larvae have the subatrium (with the closing apparatus) separated from the atrium by a length of intercalary trachea, with *Netelia* Gray being the only genus reported with the subatrium adjacent to the atrium (Short 1978). *Thibetoides aprosthemae* has the *Netelia* condition. These are exceptions to the general rule that ectoparasitoids have the subatrium separated from the atrium, while endoparasitoids have it adjacent.

Discussion

When researching the parasitoid complex of a given host, taking the opportunity to investigate the biology of the parasitoid species involved in detail, beyond just noting the host record, can often lead to surprising and interesting findings (e.g. Shaw 2017). The

parasitoid complex of *Aprosthem tardum* in our study area comprised four ichneumonid species in four genera, each of which was of exceptional interest. (A fifth species was detected just once but not reared and so could not be determined beyond subfamily). Three belong to genera that had never been reared before, and one (*L. erythrocephalus*) had just a single published host record (from *Aprosthema* sp.) but without further detail. The three lacking host records all belong to small and more or less isolated and enigmatic genera, in one case (*I. goesi*) with a confused history of subfamily placement – which can be resolved from our results – and in another (*T. quadridens*) with a past of tangled generic placement. To some extent the lack of prior biological knowledge of these taxa might be expected from the lack of research done on the rather basal and somewhat isolated host group, and the taxonomic isolation seen in the parasitoid complex of a much better-researched subfamily, Arginae, of the same host family Argidae. Thus it was no surprise that we did not rear relatively polyphagous or unspecialised parasitoids, though the lack of Tachinidae was perhaps unexpected – the more so because *Vibressa turrita* was reared from the cocoon of one of seven *Arge nigripes* (Retzius) collected as final instar larvae on *Rosa canina* at site 4. The interesting properties of the four parasitoids whose behaviour and biology we were able to study are discussed in turn below.

Lathrolestes erythrocephalus

The major surprise was the egg, which bears a kind of grappling hook at the head end. When first seen this appeared to be a single structure, but it later became clear, from a dissected-out hatched egg, that it is (or at least can be) at least three separate hooks, each carried on its own strand (Fig. 18). The egg, which darkens and toughens after being laid, becomes fastened to an internal structure of the host by means of this and it then stays put (even after hatching) during the host's larval life. Being almost black in a nearly translucent host, it is easily seen from the exterior (particularly when the host is in an early instar). Both the black visibility of the egg and its fixed position after hatching might be explained by the following facts and (substantial!) speculation: we observed that the females of *L. erythrocephalus* seem to search for hosts visually, and also appear regularly to engage in a level of superparasitism (including self-superparasitism in single visits to larger hosts) that we postulate might be adaptive (cf. van Alphen and Visser 1990) in exhausting the host's defensive response. We have seen that single eggs are sometimes encapsulated, and there is reasonable evidence that Ctenopelmatinae are always synovigenic and, in general, time-limited rather than egg-limited (Cummins et al. 2011). Heitland and Pschorn-Walcher (1992) noted a level of superparasitism much higher than would be expected by chance in several species of another ctenopelmatine tribe, Euryproctini, but in studied species of that tribe the first instar larva is surrounded by a trophamnion, which is not recorded for Perilissini. In fact these authors mention in contrast Perilissini species in which eggs seemed to be randomly distributed – unlike our belief for the perilissine *L. erythrocephalus*. As this species seems to recognise its host by sight, it seems conceivable that the visible presence of many eggs in a host, as opposed to just one or two, might deter the female from laying more eggs in such a host as, if several were already present, more eggs would almost

invariably be wasted. This would explain the conspicuously dark egg colour in adaptive terms. The fixed position of the egg chorion might be interpreted as beneficial to the first instar parasitoid larva, which we observed to be highly active and mobile within the host – presumably in search of its potential competitors which it must kill in order to survive – and we frequently saw it coming up against its own eggshell. Possibly having a fixed array, rather than a changing scatter, of already dealt-with items within the host's haemocoel aids its searching efficiency through some kind of spatial recognition, enabling it to concentrate on new items. It is otherwise very difficult to conceive of any adaptive benefit in the grappling hooks.

Biological studies on Ctenopelmatinae are rather few, as partly summarised and referenced by Broad et al. (2018). Among Perilissini, there is however considerable variation between species assigned to *Lathrolestes*. The univoltine *Lathrolestes ensator* (Brauns) is reported to have initially white but eventually black comma-shaped eggs (Zijp and Blommers 1993; Vincent et al. 2019 and references therein), though in this case eggs were essentially randomly distributed (i.e. there was neither positive superparasitism nor avoidance of it) and the egg did not hatch until the host was a cocooned prepupa in the ground. As in *L. erythrocephalus*, some *L. ensator* developed without diapause, progressing to the adult stage gradually through the winter to emerge the following spring, while others entered prepupal diapause in autumn and (under some circumstances) spent an extra year or more before becoming adult and emerging. *Lathrolestes ensator* was found in hosts as early as the first instar with an apparent preference for oviposition into the second instar, but later instar hosts were not attacked, being inaccessible. Many eggs were dissected from hosts in Zijp and Blommer's (1993) study, and no mention of any ornamentation was made. The plurivoltine *Lathrolestes nigricollis* (Thomson) was studied in complementary ways by Eichhorn and Pschorn-Walcher (1973), who figured the first instar larva and the head capsule of the final instar, and by Quednau and Guevrement (1975, as *Priopoda*) who figured the female's reproductive organs. The host is a leaf-miner and, after discovering the mine apparently at random, the parasitoid jabbed repeatedly into it, finally locating the host through its movements. Non-destructive host feeding occurred opportunistically but was not obligatory. The cucumber-shaped egg is white and no fastening structure was reported; the first instar larva hatched in from 3 to 7 days, but the authors do not say whether or not it then delays its development until the host becomes prepupal (but it would be surprising if this is not the case). Oviposition was into all instars, but especially into moderately well-grown hosts. Eggs suffered a high rate of encapsulation; although this was alleviated by superparasitism, eggs were distributed at random rather than there being a functional response. Only a proportion of first-generation offspring emerged in the same summer, the rest entering diapause as prepupae to emerge the following year, earlier than those from the second generation. Although with similar phenology, *Lathrolestes luteolator* (Gravenhorst), investigated by Carl (1976), seems to have a rather different biology and first instar larva. The female antennates the exposed host for up to a minute before ovipositing, preferring third to final host instars, less commonly attacking the second. The egg is white and bean-like, and no mention is made of any fastening device. The neonate first instar larva is said to remain partially

embedded in the egg chorion, freeing itself as it grows, and it has ventral outgrowths on abdominal segments and spines on thoracic segments as well as an unusual head structure (illustrated by Schönrogge (1991), although without mention of any continued association of the first instar larva with its egg chorion), which have not been noted in other *Lathrolestes* species by the above authors. It is also said to have a distinctively unusual head with small mandibles. As in most ctenopelmatines it delays its further (rapid) development until the host is a prepupa.

As far as we are aware, fastening devices on Ctenopelmatinae eggs have not been reported, apart from the eggs of species of *Euryproctus* Holmgren (not a Perlissini) illustrated by Schönrogge (1991) and reported also by Cummins et al. (2011) having a small stalk at the caudal pole, akin to many Tryphoninae. In the extensive survey of ovarian eggs of Ichneumonidae undertaken by Iwata (1958, 1960) none that belong to Ctenopelmatinae had any ornamentation. We dissected eggs from a female of the very large Perilissini species *Opheltes glaucopterus* for careful examination, and the 1.25 × 0.25 mm egg certainly does not bear any trace of a projecting structure. It was confirmed that the slightly wider end is the capital pole (i.e. the narrower end was directed so as to issue first from the oviduct in accordance with Hallez's (1886) Law). It is important not to conceive the appendage in *L. erythrocephalus* eggs as homologous to the stalked eggs of Tryphoninae and Lycorininae (and/or Euryproctini): quite apart from anything else, they are at different poles of the egg. They also appear to bear no relation to the more lateral modifications seen in the eggs of certain Anomaloninae (Broad et al. 2018 and references therein). If the structure of the egg of *Lathrolestes erythrocephalus* proves to be an autapomorphy, it should be borne in mind in any reclassification of Perilissini that this is the type species of the generic name *Polyoncus* Förster, 1869.

The repeated emergence of adults at times of year when no hosts would be available is noteworthy. Although captive conditions might have been contributing in some cases, it seems that asynchrony might arise naturally after *L. erythrocephalus* had entered prolonged diapause. It is possible, though we have no evidence for it, that in these cases the adult parasitoids could overwinter successfully, in view of their being synovigenic.

Ischyrocnemis goesi

The really significant discoveries regarding *I. goesi* are firstly its host, and secondly the fact that it is an endoparasitoid that kills its sawfly host in the prepupal stage typical of Ctenopelmatinae rather than Metopiinae (which are larva-pupal parasitoids of Lepidoptera, cf. Broad et al. 2018). The larval cephalic sclerites amply confirm its placement to Ctenopelmatinae, though not to any of the currently recognised tribes. As there appears to be no trophamnion surrounding the first instar larva, and as the fine ovipositor lacks a dorsal notch (Fig. 37), it is almost certainly not placeable to Euryproctini, and from our biological data, including its small eggs, we concur with Perkins (1962) and Aubert (2000) in suggesting that it would most comfortably fit in Pionini of the ctenopelmatine tribes currently recognised; although both the ovipositor having the upper valves apically swollen and the short cerci would be anomalies. However, the internal classification of Ctenopelmatinae, and even whether the subfamily as currently

understood is monophyletic, remains in doubt. The unusually strong tooth on the clypeus of adult *I. goesi* might aid the positioning of the powerful mandibles against the host cocoon as the adult cuts its way out, perhaps supporting our belief that *I. goesi* is a univoltine species always needing to deal with the tough winter cocoon of the host.

Terozoa quadridens

No biological information on *Terozoa* (= *Parablastus*) has hitherto been available. Unusual features of *T. quadridens* include regular oviposition onto the host's head capsule. Although this is known in a few other species of Tryphonini (Zinnert 1969), frequent choice of the eye is even more unusual. In such cases the behaviour of the female, once the eye is chosen as the target, is absolutely resolute. Oviposition onto the head restricts *T. quadridens* to parasitising final instar hosts as the egg would be unable to transfer through the head capsule as it is cast, in contrast to some Tryphoninae with eggs deeply anchored into the epidermis of a body segment thus allowing the egg to tear through as the host moults (see *Thibetoides*, below, and also Shaw 2001 for *Netelia*). This explains the observed behaviour of the adult parasitoid monitoring penultimate instar hosts, waiting for them to become suitable for oviposition – a behaviour reminiscent of that of the campoplegine ichneumonid *Hyposoter horticola* (Gravenhorst) which oviposits into first instar larvae of the nymphalid butterfly *Melitaea cinxia* (Linnaeus) just before they hatch, having monitored the developing egg batches of the host for the previous several days (Nouhuys and Kaartinen 2008). Egg placement on the host's head presumably dictates that the first instar *T. quadridens* larva must leave the eggshell and move to softer tissue before it can commence feeding. It is interesting that in none of our six female specimens (all killed by deep-freezing prior to immersion in ethanol) is there an egg exposed on the ovipositor (in three of our 6 dead specimens the egg can be discerned in the hypopygium and the stalk is just visible), unlike the several illustrations of females of *Terozoa* species in the literature (Kasparyan and Tolkanitz 1999; Kasparyan 2019a), which we presume must be of females that had experienced a less peaceful, chemically convulsion-inducing death. Holding the egg back in life may be necessary in view of its anchor being so tiny and stud-like: we never saw eggs held ready on the ovipositor in the living females seen searching or ovipositing, but rather it appeared to take some effort to force the egg through the hypopygium during the oviposition process, suggesting that the egg may not have fully emerged from the oviduct beforehand. Against this, however, is the strong concertina movements of the apex of the metasoma seen in the videos immediately after oviposition, that might signify re-arming with another egg. The quadridentate mandibular structure of *T. quadridens* must be a specialization aiding emergence by cutting through the particularly tough strands of the (inevitably) winter cocoon of the host.

Thibetoides aprosthemae

Preferential parasitism of the host in an early instar (it seems that attempted oviposition on later instars is generally unsuccessful) is very unusual in Tryphonini (Bennett

2015), and the apparently rather precise and consistent egg placement, low down behind the third (or sometimes second) thoracic leg, is also notable.

Larval spiracles and a reinterpretation of their closing apparatuses

Prior to this study, the closing apparatus had been regarded by the one of us (DBW) concerned with larval morphology as a pair of bow-like longitudinal structures found below the atrium and before the onset of the coarsely annulated spiracular trachea (Fig. 79A, B). The sections of trachea containing the closing apparatus typically had finer annulations than the following spiracular trachea. Sometimes a section of coarsely annulated trachea (similar to the spiracular trachea) was seen between the atrium and closing apparatus (Fig. 79A). Short (1978: 124) summarized what was known about the distribution and possible functions of these morphologies: "*The closing apparatus of the spiracle adjoins the atrium in most endoparasites, whereas in ectoparasites it may adjoin the atrium or be situated some distance from the atrium. There are no obvious explanations for this. It is generally assumed that the spiracles are open in endoparasites in the final larval instar which is carnivorous, feeding on the tissues of the host and liberating air from its tracheae. If the spiracle is open there is possibly some biological advantage in having the closing apparatus situated close to the atrium. If one function of the closing apparatus is to prevent the entry of body fluids of the host into the tracheal system, then it is best situated to perform this function when it adjoins the atrium. If, however, such a precaution were necessary, one would more readily expect to find hydrofuge structures at the opening of the tracheal system, as in many aquatic insects.*" This is the only published speculation on the function of the closing apparatus. We and others had never closely considered how the closing apparatus actually functioned, vaguely supposing it was some sort of valve; Andrew Bennett (pers. comm.) said that he "*just assumed that the thin longitudinal structure was some sort of muscle or tendon that attached to the distal end of the trachea and somehow constricted the spiracle to close it.*"

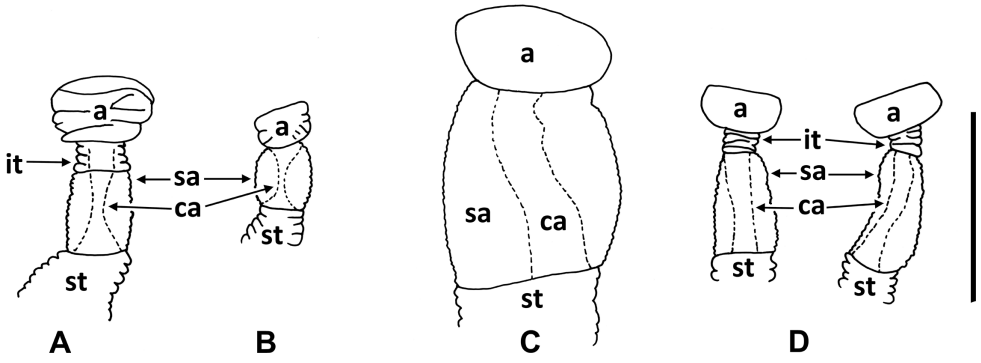


Figure 79. Final instar larval spiracles of Ichneumonidae **A** *Xorides rileyi* (Ashmead); NMNH, Short slide #076 **B** *Lissonota laticincta* Townes; NMNH, DBW 18.vii.1986d **C** *Chasmias sclestus* (Cresson); NMNH, Short slide #240 **D** *Alomya semiflava* (Stephens); ANIC. a = atrium, ca = closing apparatus, it = intercalary trachea, sa = subatrial area, st = spiracular trachea. Scale bar: 0.1 mm.

We were therefore surprised to find that the three ctenopelmatine species in this study (*Lathrolestes erythrocephalus*, *Ischyrocnemis goesi*, Ctenopelmatinae sp. X) lack a closing apparatus, and that this state is apparently widespread in ctenopelmatines (see comments under *L. erythrocephalus*). This led us to consider the closing apparatus in larval ichneumonids more closely. As far as we can determine, the term was first used by Beirne (1941). He provided a set of detailed drawings (his fig. 3) and said that the closing apparatus was either thick-walled or thin-walled. From his drawings, the thick-walled type gave the appearance of the longitudinal structures whilst the thin-walled type was just a simple cylinder (his m, n, p, q). This interpretation was accepted by Thelma Finlayson in her numerous papers treating ichneumonid larvae, and apparently by Short (1959, 1978) by his use of 'thin walled' to describe ctenopelmatine spiracles (although he then depicted internal longitudinal structures).

There are problems, however, with accepting the appearance of the closing apparatus to be the result of tracheal wall thickness. Looking at larger specimens such as *Xorides rileyi* (Ashmead) (Fig. 79A), the longitudinal structures can often be traced up into the section of trachea that separates Beirne's closing apparatus from the atrium. Yet more troubling are the cases where there are clear indications of internal spines in the closing apparatus. Banchini exhibit this, and although some genera (*Banchus* Fabricius, *Ceratogastra* Ashmead, *Philogalleria* Cameron) lack longitudinal internal structures, others such as *Exetastes* Gravenhorst do have them (Wahl 1988). NMNH slides of *Exetastes* show this very clearly: *E. illinoiensis* (Walsh), *E.* ?*bifenestratus* Cushman (Short slides 188 and 190) and *E.* sp. (DBW 31.x.1985k). The section of trachea containing the longitudinal structures are flask-shaped and the walls in cross-section are thin, not thickened (Wahl 1988: figs 6–7). Some of the longitudinal structures are distinctly bent or otherwise off the median axis. It would seem that a better model for the closing apparatus is a tube that runs from the spiracular trachea to the atrial base, thus accommodating internal spines in the finely-annulated section of trachea that surrounds it. Another striking specimen is *Metopius dentatus* (Fabricius) (NMNH, Short slide 158). The subatrial region is spinose and what is clearly a tube runs from the atrium to the spiracular trachea. Several of the spiracles have the tube constricted and off-center, and one has the tube apparently expanded and partially contiguous with the tracheal wall.

More evidence for the closing apparatus being a tube is found in the Ichneumoninae. Ichneumonine larvae are highly derived (Bennett et al. 2019; Santos et al. 2021: supplementary material S8), yet since DBW was not interested in spiracular morphology, he had ignored (Sime and Wahl 1998; Bennett et al. 2019) one of their most interesting features: the heavily spinose region below the atrium, discussed in detail by Gillespie and Finlayson (1983) as the closing apparatus. Gillespie and Finlayson illustrated the spiracles of 42 ichneumonine species but did not show internal longitudinal structures (evidently considering them to have closing apparatuses of the 'thin-walled' type). Conversely, Short (1978) illustrated the spiracles of 111 species and showed longitudinal structure within all of them. DBW was able to examine 21 of Short's slides and nine of Gillespie and Finlayson's. The slide of *Alomya semiflava* Stephens (Hinz and Short 1983), the sister group to the rest of the Ichneumoninae (Bennett et al. 2019; Santos et al. 2021), was also to hand. *Alomya semiflava* has: (i) the area below the atrium with internal

spines, and (ii) unmistakable longitudinal structures in that region (Fig. 79D). Of the 21 Short species, 14 show internal longitudinal structures. Gillespie and Finlayson slides show the internal structures in 4 species. Additional specimens [NMNH, EMUS] showing similar internal structure were also examined: *Araeoscelis* spp., *Gnamptopelta obsidianator* (Brullé), *Holcojoppa mactator* (Tosquinet), *Mokajoppa respinozai* Ward and Gauld, *Pedinopelte* sp., and *Psilomastax pyramidalis* Tischbein. In all cases, the longitudinal structure resolves as a tube within a spinose subatrial region (similar to Fig. 79C). *Gnamptopelta obsidianator* and *M. respinozai* have the tube itself distinctly spinose. Most ichneumonine specimens have the tube presenting as lacking in the majority of spiracles. This appears to be due to two factors: (i) the tube is apparently rather weakly attached to the atrium, and (ii) the tube continues down into the spiracular trachea, where it presumably merges at some point. Between these two aspects, the tube is often detached and retracted down the spiracular trachea – either from the moult from larva to pupa or the stretching and manipulation of the exuviae during slide mounting. As to why Short and Gillespie and Finlayson were at such odds in what they portrayed, Robertson Davies said it best: "… *the eye sees only what the mind is prepared to comprehend*".

It is hard to believe that the longitudinal structure in most ichneumonid larval spiracles is the result of thickened tracheal walls, whilst the Ichneumoninae, Banchini, and *Metopius* have intraspiracular tubes. Instead it seems simpler to judge that Beirne misinterpreted what he saw. In short subatrial sections, the tube is broad where it meets the spiracular trachea, narrows in the middle, and then expands again at the atrial base – giving the impression of thickened walls that are internally convex. We propose a new spiracular terminology based upon the work of Michener (1953), who introduced morphological terms used throughout the aculeate community. The new usage is illustrated in Fig. 79. The finely annulated section of trachea below the atrium is the 'subatrial area'. It connects with the more coarsely annulated 'spiracular trachea'. If a coarsely annulated tracheal section occurs between the atrium and subatrial area, this is known as the 'intercalary trachea'. The 'closing apparatus' is now defined as a tubular structure running within the subatrial area and connecting the atrium and spiracular trachea.

How the closing apparatus functions to regulate moisture loss (for ectoparasitoids) or fluid ingress (endoparasitoids) is an open question. A survey of Short's NMNH slides reveals that the higher Ophioniformes (Cremastinae, Anomaloninae, Ophioninae, Campopleginae; Bennett et al. 2019) all lack a closing apparatus (Short generally drew them with a closing apparatus present, at least in a rudimentary fashion). This clade of larval endoparasitoids (larval-pupal in the case of anomalonines) comprises a large and successful radiation, despite this lack of a closing apparatus.

Concluding remarks

The parasitoid complex of *Aprosthema tardum* is highly specialised, in that respect comparable to (but very different from) the specialisation seen in parasitoids of the much better studied argid subfamily Arginae. Here we found that three of the four species studied belonged to enigmatic or rather morphologically extreme genera of previously completely

unknown biology; a fourth species had unique features of its egg not hitherto discovered. This suggests that there may be good prospects of discovering the unknown, and perhaps equally fascinating, biology of small and little-known genera of parasitoids by investigating other groups of Argidae. For example, a recent paper (Zwakhals and Blommers 2022) records rearing for the first time the distinctive Tryphonini species *Neleges proditor* (the only species of its genus) from the sterictiphorine argid *Sterictiphora geminata*.

It is of interest that *Terozoa* (= *Parablastus*) and *Thibetoides* have been regarded as close relatives (Bennett 2015 and references therein), although the differences in biology (including egg structure) reported here in using the same host species are large and at first sight might suggest different evolutionary origins. Several morphological peculiarities are seen in the ichneumonids known to parasitize argid sawflies, including head structures that might be adaptations for escaping from the unusual structure of the host cocoon (inside which they all pupate), and in particular the very tough fibres of the winter cocoon. These include mandibles with both teeth (*Terozoa*, Fig. 63) or the upper tooth (*Thibetoides*, Fig. 77) divided, or both teeth with strong internal flanges (*Lathrolestes erythrocephalus*, Fig. 25 – remarkably reminiscent of *Ophion* spp. (Ophioninae); seen also but to a much lesser extent in the mandible of *Ischyrocnemis* (Fig. 39)), and the clypeus with either an apical tooth (*Ischyrocnemis* (Fig. 39) and *Scolobates*) or a pair of subapical tubercles (*Neleges* and to a lesser extent *Boethus* Förster); Zwakhals and Blommers (2022) speculate on the function of the clypeal tubercles in *Neleges*. While *Ischyrocnemis*, *Thibetoides*, *Terozoa* and *Neleges* all have some sort of process on or just below the frons, in all but the last of these as the culmination of a more or less developed frontal carina, it is less compelling (though possible) that these structures also aid escape from the host cocoon. It is of interest that some of the various presumed specialisations mentioned above are inconsistent (e.g. clypeal tooth, or pair of tubercles), though some may be convergent (e.g. tendency for divided mandibular teeth; armature of frons).

Our parasitoid complex appeared to include some species that were present in all host generations while others are apparently more phenologically restricted. This has been noted in a few parasitoid complexes (Shaw 2017 and references therein), but it is unusual. Whether or not it might have a bearing on the possibility of local exclusions could only be answered by much more data collected systematically over several years, but it seems likely that temporary patch extinctions of some of the scarcer parasitoids might be caused by the excessively abundant and strongly plurivoltine *L. erythrocephalus*, which is certainly an effective intrinsic competitor at least over the two ectoparasitoid Tryphoninae. However, the fact that we did not find all species of parasitoid at all locations might merely reflect insufficient sampling.

We lack data for *T. aprosthemae*, but in general it is clear that superparasitism is not avoided by *L. erythrocephalus*, *I. goesi* or *T. quadridens* (indeed, it appears to be deliberate in *L. erythrocephalus*). In cases of multiparasitism between an ectoparasitoid and an endoparasitoid a frequent outcome was the death of all, but when one survived it was generally the endoparasitoid by virtue of its faster development once the host reached its prepupal stage. A single instance in which *T. quadridens* developed to the cocoon stage from a host containing an egg of *L. erythrocephalus* probably depended on the (unrelated) encapsulation of the endoparasitoid, which was certainly commonplace

although we did not see direct evidence in this case. We reared adults of *L. erythrocephalus* from hosts also parasitised by each of the other three species, and *I. goesi* from a host also parasitised by *T. quadridens*. Multiparasitism by the endoparasitoids rarely, if ever, led to the death of the host before either could develop; no reliable information on competition between *L. erythrocephalus* and *Ischyrocnemis goesi* was obtained, but it seems likely that, as in most cases of competition between endoparasitoids, the earliest first instar larva to hatch would usually succeed in killing later-developers.

In addition to clearly high levels of parasitism, *Aprosthema tardum* appears to suffer often substantial levels of predation from ants. We have found that in some suitable-looking areas with plenty of *Laythyrus* (for example La Garidelle in Site 2) where ants such as *Camponotus cruentatus* (Latreille), *Camponotus vagus* (Scopoli) and *Crematogaster scutellaris* (Olivier) were dominant, *A. tardum* larvae disappeared quickly and we were generally unable to find large larvae or summer cocoons. In contrast, in places where *Formica fusca* Linnaeus was dominant, the sawfly seemed to have a much better chance of reaching maturity, even though this ant is known to take a wide range of invertebrates (Lebas et al. 2016). However, *F. fusca* was not only observed to be uninterested in *Aprosthema* larvae, even when contact was made, but also it tended to displace the more aggressive ant species; Lebas et al. (2016) note that it defends resources from other ants. *Lasius niger* (Linneaus) is also known to attack *Aprosthema* larvae (Vikberg 2004; Liston et al. 2018), but was largely absent from our sites, although potentially causing a problem in the more domestic situation, where the captive rearing was done, when *Aprosthema* larvae descended to make cocoons. Any attempt to understand the population dynamics of *A. tardum* would clearly need to take into account the role of ants, and probably also *Polistes* species (Vespidae) which we have seen taking the larvae, as well as parasitoids.

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