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The life-history of *Aprosthema tardum* (Klug, 1814) (Hymenoptera, Tenthredinoidea, Argidae)

With 19 figures and 2 tables

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Abstract

Aprosthema species are usually rarely found. In recent years, in southern France, relatively strong populations of *A. tardum* were detected, which allowed observations on the behaviour and development of the species to be made. The host plant in the study area is *Lathyrus latifolius* (Leguminosae). As in a few other *Aprosthema* species, whose development has been previously investigated in northern Europe, *A. tardum* is bivoltine, although a partial third generation may occur in southern Europe under favourable weather conditions. Adults display seasonal dimorphism, similar to that already described for *A. melanurum.* Individuals which overwinter make stronger cocoons in the soil (winter cocoons), whereas the more loosely spun cocoons (summer cocoons) of individuals which complete their whole development in a single season are usually found on aerial parts of the host, or plants of other species growing near to the host. The head behind the eyes is more strongly developed in adults which emerge from winter cocoons. A few individuals of *A. tardum* in the first generation, which normally form summer cocoons, make winter cocoons and enter prolonged diapause, like almost all larvae of the second generation. During oviposition the valvulae 3 are deployed so that their inner surfaces are in very close contact with the leaf epidermis. We suggest that this behaviour is connected to the presence of spines on the valvula inner surface. The latter are found in many argid sawflies, but not in other families of Palaearctic Tenthredinoidea, in which the valvulae have not been observed to be used in a similar way.

Key words

Lathyrus latifolius, voltinism, seasonal dimorphism, oviposition, valvula 3 structure and function

Zusammenfassung

Aprosthema-Arten sind in der Regel selten zu finden. In den letzten Jahren wurden in Südfrankreich relativ starke Populationen von *A. tardum* nachgewiesen, die Beobachtungen über das Verhalten und die Entwicklung der Art ermöglichten. Die Wirtspflanze im Untersuchungsgebiet ist *Lathyrus latifolius* (Leguminosae). Wie bei einigen anderen *Aprosthema*-Arten, deren Entwicklung zuvor in Nordeuropa untersucht wurde, ist *A. tardum* bivoltin, wobei eine teilweise dritte Generation in Südeuropa unter günstigen Wetterbedingungen vorkommen kann. Imagines zeigen saisonalen Dimorphismus, ähnlich dem bereits für *A. melanurum* beschriebenen. Individuen, die überwintern, bilden stärkere Kokons im Boden (Winterkokons), während die lockereren Kokons (Sommerkokons) von Individuen, die ihre gesamte Entwicklung in einer einzigen Saison vollenden, gewöhnlich an oberirdischen Teilen des Wirts oder an

Pflanzen anderer Arten anzutreffen sind, die in der Nähe des Wirtes wachsen. Der Kopf hinter den Augen ist bei Imagines, die aus Winterkokons schlüpfen, stärker entwickelt. Einige Individuen von *A. tardum* in der ersten Generation, die normalerweise Sommerkokons bilden, bilden Winterkokons und treten, wie alle Larven der zweiten Generation, in eine verlängerte Diapause ein. Während der Eiablage treten die gesamten inneren Oberflächen der Valvulae 3 in sehr engen Kontakt mit der Blattepidermis. Wir vermuten, dass dieses Verhalten mit dem Vorhandensein der inneren, mit Dornen besetzten Oberfläche der Sägescheide zusammenhängt. Diese Dornen finden sich bei vielen Arten der Argidae, nicht aber bei anderen paläarktischen Tenthredinoidea-Familien, für die man eine ähnliche Verwendung der Valvulae 3 nicht beobachtet hat.

Introduction

The sawfly genus *Aprosthema* occurs mainly in the Palaearctic, with a few species in the Oriental and Nearctic Realms (Taeger et al. 2010). The taxonomy of the Palaearctic species is still poorly understood. Progress has been hampered by a general scarcity of material, compounded by confusion caused by the seasonal dimorphism exhibited by adult specimens of both sexes (Vikberg 2004). The differences affect mainly head morphology, particularly the size and shape of the parts of the head behind the eyes, and the length of the antennal flagellum. It is thought that the larger head dimensions of overwintered adults are connected to their better developed mandibular muscles, needed to bite their way out of a cocoon that has more solid walls than the loosely spun cocoon of the summer-emerging individuals (Vikberg 2004). The latter author demonstrated that three European species display such seasonal dimorphism: *melanurum* (Klug, 1814), *fusicorne* (Thomson, 1871), and *intermedium* (Zaddach, 1864). At least in *A. melanurum*, adults of the summer generation also exhibit a paler body colour pattern than adults from overwintered cocoons.

One species has been relatively abundant during recent years at several localities in the South of France. The main impetus for examining some aspects of its natural history was the rearing by the second and third authors, on 29.v.2014, of a species of *Thibetoides* (Hymenoptera: Ichneumonidae, Tryphoninae), since described as *T. aprosthemae* Shaw (Shaw et al. 2018), from an *Aprosthema* cocoon collected at Taradeau, in our study area. On 11.v.2014, this cocoon had been found on a leaf of that year's growth of *Knautia arvensis* (L.) Coulter.

We next asked which species of *Aprosthema* was the host of *Thibetoides*, and where to look for its larvae. Noblecourt (2016) listed seven *Aprosthema* species from France, but the status of two of these was assessed as needing clarification. All available host plant records for the genus involve herbaceous Leguminosae (= Fabaceae) species. Aware of this, the second and third authors started to look closely at the most likely potential host plant species, but it was not until 30.v.2016 that they first found larvae of *Aprosthema*, on leaves of *Lathyrus latifolius* L. From these five larvae, one male was reared on 13.vi.2016, which was identified as *Aprosthema tardum* (Klug, 1814) by the first author. The cocoon of this male was identical to the cocoon from which the holotype of *Thibetoides aprosthemae* had been reared (Shaw et al. 2018).

Material and methods

The identification of *Aprosthema tardum* by the first author was made using the adult morphological characters described by Vikberg (2004). Adults, larvae and cocoons of *Aprosthema tardum* were collected by the second and third authors at localities (Table 1) mostly in Département Var, France, from April through July, in 2016 and 2017. The abbreviation in Table 1 before each locality name is used in the rearing notes. All the observed and collected larvae were feeding in nature on the leaves of *L. latifolius* L. (Leguminosae). Larvae kept for rearing were placed in a container, with a water-filled bottle buried in soil to hold cut shoots of the food plant. The containers were kept in a garden shed, or outdoors in a shaded spot, at more or less ambient temperatures. From these rearings some adults emerged, and some died in their cocoon, mostly before pupating (Table 2). In two cases the larva had been parasitized, and an ichneumonid cocoon was formed in the host cocoon, from one of which a still unidentified adult Ctenopelmatinae parasitoid emerged. Although newly emerged females of *A. tardum* have been put in the same container with an older male, copulation has never been observed. Many observations of larvae, cocoons or adults, have been filmed (Kan-van Limburg Stirum & Kan 2018). Voucher specimens are deposited in the National Museums of Scotland, Edinburgh (NMS) and the Senckenberg Deutsches Entomologisches Institut, Müncheberg (SDEI). The adults and larvae are labelled with the code BVLS (abbreviation for Brigitte van Limburg Stirum), followed by a number.

Lathyrus latifolius is very common in Var, growing nearly everywhere along verges and forest trails, but also in open fields and gardens (see Table 1). It can get through mild winters, in sheltered and humid places, without the above-ground parts dying off. From March onwards, young shoots and new leaves are formed.

Tab. 1: Localities at which specimens of *Aprosthema tardum* were collected, and observations made. The French localities are mainly on forest trails, partly through areas of rough grassland, surrounded by dry forest dominated by *Pinus* and *Quercus*. Most of the observations were made, and the majority of specimens collected, at Taradeau (TA) (Fig. 18), which is a typical habitat. This is a rather small area comprising a linear fire-break of slightly disturbed limestone grassland and scrub (half of the strip being mown along its length in alternate winters), within a moderately open, mixed, dry forest at low altitude.

Abb.	Country / locality name	Latitude	Longitude	Altitude a.s.l.	Habitat
	France, Var				
TA	Taradeau, Dom. Ott	43.293°N	6.256°E	200–212 m	linear field
BA	Bargemon	43.371°N	6.321°E	589 m	roadside verge
BP	Bargemon, Le Plan	43.370°N	6.335°E	351 m	garden
BF	Bargemon, Favas	43.371°N	6.315°E	623 m	small field
CG	Callas, Gariedelle	43.334°N	6.336°E	260 m	forest trail
CL	Clavier	43.354°N	6.340°E	287 m	forest trail
	Italy, Imperia				
AP	Apricale	43.534°N	7.391°E	302 m	wild garden

Results

Seasonal dimorphism in adult *A. tardum*

Differences in the head morphology of winter and summer generations are rather pronounced, particularly in females, and similar to the dimorphism described by Vikberg (2004) in *A. melanurum*. The differences are best seen in dorsal view. In both sexes (females Figs 1 & 2, males Figs 3 & 4), the length of the head behind the eyes is reflected in the proportions of the postocellar area: in summer generation individuals it is shorter (about 1.5× as long as the diameter of a lateral ocellus: Figs 1 & 3) than in overwintered individuals (about 2.0× as long as the diameter of a lateral ocellus: Figs 2 & 4). Also, the profile of the head behind the eyes of summer generation females (Fig. 1) appears clearly contracted compared to the expanded profile of winter generation females (Fig. 2). As noted by Vikberg (2004) for *A. melanurum*, the antennal flagellum of both sexes of *A. tardum* is clearly longer in the overwintering morph than the summer morph, but we did not attempt to quantify this difference, because too few specimens were available.

Colour differences between adults of the winter and summer generations of *A. tardum* are slight. In both sexes, the bases of the femora of the summer generation are paler: the metafemur can be almost entirely pale in the summer morph, whereas the basal half is typically black in the winter morph. The valvulae 3 of the ovipositor are usually laterally pale in summer morph females, whereas entirely black in the winter morph.

2016 rearings and observations

TA: On 30.v.2016, five larvae (Figs 16–17) were collected from three different host plants. After four days (on 3.vi.2016) one larva spun an open, light-coloured cocoon of about 10 mm on a leaf of the host plant (summer cocoon, Figs 5, 7). Ten days later (13.vi.2016) a female emerged (BVLS024). The four other larvae crept off the host plant to make a cocoon in the litter layer. These cocoons were spun more tightly and had a brownish colour (winter cocoons, Fig. 6). They were kept outside in the shade through the winter, in the same container. The mature larva leaves a typical “stepped” feeding pattern on the leaf (Fig. 8). At the end of February of the following year (26.ii.2017) one male emerged (BVLS039). We tried to keep this male alive, with honey-water, until a female might emerge with which mating could be induced. The male died after 8 days (6.iii.2017), and no female had emerged. Some days later (9.iii.2017) a female emerged (BVLS040). We also kept this female alive, hoping that another male would emerge. Nine days later (18.iii.2017), when we put fresh *L. latifolius* leaves in the container, the female started egg-laying in the leaves without copulation (Figs 9–11). After 8 days (26.iii.2017) one neonate larva (1 mm) was feeding on one of the leaves. Until May nothing had emerged from the other two cocoons. We opened them and found one to contain a dead female, and the other a dead, dried larva.

On 13.vi.2016 a larva of 16 mm was collected from its host plant. The next day it made a winter cocoon in a *Lathyrus* flower in the bottom of the container. Almost a year later, on 27.iii.2017 a male emerged (BVLS042).

Tab. 2: Specimens of *Aprosthema tardum* collected in cocoons in the field, or reared indoors from larvae at least until a cocoon was made. Locality names (Loc.), see Table 1. Lengths of larvae were measured when they were nearly mature. Additional notes on specimens (No.):
2, 3, note the rather wide span in emergence dates. 3, the development period of the egg, laid on 18.iii.2016 and hatched on 26.iii.2016, is about 8 days. 11, 12, the late dates suggest that these may represent a partial third generation. 13, 19, both larvae had been parasitized by, most probably, the same species of ctenopelmatine endo-parasitoid. These parasitized larvae made their winter cocoons on the host plant leaves. 20, 21, the development of these larva, between hatching, 23.iv.2017, and making a cocoon, 9.v.2017, took about 16 days, under normal summer weather conditions, and nearly the whole development was completed using a single leaf. 27, possibly belongs to the second generation, but emerged in same year.

Loc.	No.	Collection date	Length larva	Cocoon spinning date	Cocoon type	Date emerged	Sex	Code
		2016						
TA	1	30.v.2016	? mm	3.vi.2016	Summer cocoon	13.vi.2016	♂	BVLS024
	2	30.v.2016	? mm	7.vi.2016	Winter cocoon	26.ii.2017	♂	BVLS039
	3	30.v.2016	? mm	7.vi.2016	Winter cocoon	9.iii.2017	♀	BVLS040
	4	30.v.2016	? mm	7.vi.2016	Winter cocoon	dead v.2017	♀	-
	5	30.v.2016	? mm	7.vi.2016	Winter cocoon	dead v.2017	larva	-
TA	6	13.vi.2016	16 mm	14.vi.2016	Winter cocoon	27.iii.2017	♂	BVLS042
BP	7	3.vii.2016	?	?	Summer cocoon	? vi.2016	?	BVLS026
CG	8	6.vii.2016	15 mm	Searching for place to spin 7.vii.2016	?	Attacked by ants: dead vii.2016	larva	BVLS027
BA	9	8.vii.2016	16 mm	Searching for place to spin 10.vii.2016	?	Attacked by ants: dead vii.2016	larva	BVLS030
	10	8.vii.2016	15 mm	11.vii.2016	Winter cocoon	dead v.2017	larva	-
BF	11	8.vii.2016	?	?	Summer cocoon	? vii.2017	?	BVLS028
	12	8.vii.2016	?	?	Summer cocoon	? vii.2017	?	BVLS029
CL	13	9.vii.2016	16 mm	10.vii.2016	Winter cocoon	parasitized	-	PTLK347
BP	14	11.vii.2016	16 mm	12.vii.2016	Winter cocoon	dead v.2017	♂	-
		2017						
TA	15	23.iv.2017	14 mm	27.iv.2017	Summer cocoon	7.v.2017	♂	BVLS057
	16	23.iv.2017	15 mm	28.iv.2017	Summer cocoon	12.v.2017	♀	BVLS063
	17	23.iv.2017	15 mm	28.iv.2017	Summer cocoon	12.v.2017	♀	BVLS064
TA	18	28.iv.2017	15 mm	29.iv.2017	Summer cocoon	9.v.2017	♀	BVLS058
	19	28.iv.2017	15 mm	29.iv.2017	Winter cocoon	parasitized: a female ctenopelmatine emerged 18.iv.2018	-	BVLS085
TA	20	3.v.2017	15 mm	9.v.2017	Summer cocoon	20.v.2017	♀	BVLS072
	21	3.v.2017	15 mm	9.v.2017	Summer cocoon	21.v.2017	♀	BVLS073
TA	22	22.v.2017	16 mm	25.v.2017	tried, but failed	dead v.2017	larva	BVLS090
	23	22.v.2017	16 mm	24.v.2017	Winter cocoon	dead ii.2018	larva	BVLS091
	24	22.v.2017	16 mm	24.v.2017	Winter cocoon	dead ii.2018	larva	BVLS092
	25	22.v.2017	16 mm	24.v.2017	Winter cocoon	12.iii.2018	♂	BVLS093
	26	22.v.2017	16 mm	24.v.2017	Winter cocoon	14.iii.2018	♂	BVLS094
AP	27	8.vi.2017	?	?	Summer cocoon	15.vi.2017	♀	BVLS084
BP	28	27.vi.2017	15 mm	1.vii.2017	Winter cocoon	Early February 2018	♂	BVLS089

Oviposition: Observations were done on wild females in TA and on a reared female (BVLS040). Six successful ovipositions were filmed, making it possible to observe some details more accurately than could have been achieved by only visual observation in the field (see Kan-van Limburg Stirum & Kan 2018). Under natural conditions, the female mostly flies between leaves which are potential oviposition sites. After landing on a leaf, she walks to its apex and turns (if necessary), then starts to move towards the base of the leaf, along one of the margins. In all cases, oviposition was into the margin of the leaf. Leaves which had not yet unrolled seemed to be favoured. Two eggs were often laid in a single leaf. In one case, two oviposition events into the same rolled leaf were separated by an interval of only 2–3 seconds, during which the female withdrew her saw and took a few steps towards the base of the rolled leaflet in order to lay a second egg, only about 5 mm distant from the first. The laying of one egg took about 60 seconds, in both cases.

A single oviposition comprises three phases:
1 (ca. 26 seconds), valvulae 3 and ventro-apical part of abdomen in close contact with plant epidermis, the valvulae spread widely apart, with each inner surface pressed against the leaf. Conspicuous movements of abdomen, but other body parts move only slightly along plane vertical to body.
2 (ca. 50 seconds), tip of abdomen raised, so that only hypopygidial area remains in contact with leaf (Fig. 9). The valvulae remain widely open. Body movements similar to phase 1.
3 (ca. 14 seconds), tip of abdomen again lowered, and valvulae 3 inner surfaces in close contact with leaf (Fig. 10). Movement of abdomen less obvious than phases 2 and 3, but anterior of body sways slightly from side to side.
In phases 1 and 2, if the leaf is unfolded, the valvulae 3 clasp the leaf margin, but if the leaf is still rolled, the valvulae are splayed almost flat against the epidermis, with their ventral edges rotated outwards, on each side of the leaflet margin.

BP: On 3.vii.2016 many leaves of *L. latifolius* displayed the typical feeding pattern of *A. tardum* larvae (Fig. 8). On one of these leaves an empty (summer) cocoon (BVLS026) was found. The summer cocoons are only superficially glued to the leaves, and may be dislodged fairly quickly by wind or rain.

CG: On 6.vii.2016 a larva (15 mm) was found on the food plant. The next day this larva had gone to the bottom of its container to make a cocoon, but a large number of ants, *Lasius niger* (Linnaeus, 1758), had managed to enter the container and attack the larva, which did not survive the onslaught (BVLS027). This is remarkable, as we have regularly seen, in the natural environment, different ant species walking on leaves without paying any attention to *Aprosthema* larvae when they occurred on the same leaves.

BA: On 8.vii.2016 two larvae (11 mm and 16 mm) were collected from the same *L. latifolius* plant. On 10.vii.2016 the largest left the food plant to make its cocoon. We wanted to film this outside in the field, but as soon as it was on the ground in the vegetation it was suddenly fiercely attacked by ants coming from every direction, and was killed (BVLS030).

Three days later (11.vii.2016), when the second larva was around 16 mm long, it left the food plant and made a winter cocoon at the bottom of the container, in which it was kept during the winter. No adult emerged and in May 2017 a dead dry larva was found inside the cocoon.

BF: Although on 8.vii.2017 no larvae were found, many leaves of *L. latifolius* showed the typical feeding marks, and two empty summer cocoons on leaves were collected (BVLS028–29).

CL: On 9.vii.2016 a larva of 16 mm was collected. This larva directly made a winter cocoon under a leaf at the bottom of the container (PTLK347). In the following year, on 29.vi.2017, a second cocoon inside the winter cocoon was visible (Fig. 12). It seemed that this larva had been parasitized by an endo-parasitoid, most probably of the ichneumonid subfamily Ctenopelmatinae (M. R. Shaw, personal communication). When in September no adult had emerged, the sawfly cocoon was cut open, revealing a parasitoid cocoon (a dead parasitoid prepupa inside) and the host skin (Fig. 13). These cocoons were sent to Mark R. Shaw for identification, who forwarded them to the first author to attempt to obtain a CO1 (barcode) DNA sequence, which might enable determination of at least the parasitoid subfamily. Unfortunately, no parasitoid DNA was isolated from these remains.

BP: At the same spot where on 3.vii.2016 an empty summer cocoon was collected, on 11.vii.2016 a larva 16 mm long was collected, which the next day made a winter cocoon. In May 2017 no adult had emerged, so the cocoon was opened. It contained a dry, dead male.

2017 rearings and observations

TA: On 23.iv.2017 three larvae (around 12 mm) from the same host plant were collected. Four days later (27.iv.2017) one larva (15 mm) made a summer cocoon on a leaf, from which, 10 days later (7.v.2017) a male emerged (BVLS057, NMS). This male was kept alive for 10 days. When two days later a female (BVLS058) emerged, it was introduced to the container holding the male. We kept them together for a couple of days, but no mating or even attempted pairing was observed. On 28.iv.2017, the other two larvae each made a summer cocoon on a leaf of the food plant. These two cocoons were placed for some days (until 1.v.2017) back in the vegetation where the larvae came from, to see if they would be parasitized by *Thibetoides*. 14 days (12.v.2017) after the cocoons were made, two females (BVLS063–64) emerged.

On 23.iv.2017, two larvae of about 10 mm were found feeding on the same plant, on different leaves. They were collected five days later, on 28.iv.2017 (15 mm). The next day (29.iv.2017) each larva made a cocoon. One larva made a summer cocoon and ten days later a female emerged (BVLS058, NMS). The other larva made a winter cocoon under a leaf at the bottom of the container. In September a second cocoon was visible inside the first, which indicated that this larva has been parasitized by an endo-parasitoid (BVLS088). On 9.ix.2017 the cocoon was cut open. The still living parasitoid prepupa and the host skin looked very similar to PTLK347 (Table 2). On 18.iv.2018 a female Ctenopelmatinae (Ichneumonidae) emerged, which will be sent to Mark R. Shaw for identification.

On 23.iv.2017, two newly hatched larvae (2 mm) on the same leaf were observed and filmed (Figs 14–15). The development of these larvae was followed over a number of days. Repeatedly, it was observed that different species of ants inspected the leaf without attacking the larvae. After ten days (on 3.v.2017) these two larvae (12 mm) were collected. After day six (9.v.2017) each made a summer cocoon on a leaf. They had been feeding on the same leaf during almost their entire development. Only in the last days, before making a cocoon, had they fed on another leaf. Their larval development had lasted about 16 days. These cocoons were also placed back at the spot where the larvae were collected, for a couple of days (until 17.v.2017), to see if they would become parasitized. After respectively 11 and 12 days, on 20.v.2017 and 21.v.2017, two females emerged (BVLS072–73). On 22.v.2017 the females were released at the place where they were collected. They immediately started ovipositing in the leaves of the host plant.

On 22.v.2017 five larvae were collected (around 16 mm). Four made winter cocoons on 24.v.2017, and one failed to make a cocoon and is now dry (BVLS090). The cocoons have been under observation since 16.ii.2018. Two larvae died in their cocoon (BVLS091 & 92), and two males emerged on 12.iii.2018 and 14.iii.2018 (BVLS093 & 94).

AP: On 8.vi.2017, on a big *Lathyrus latifolius* plant with leaves showing the typical feeding patterns of *Aprosthema tardum* larvae, we found a summer cocoon on a leaf. On 15.vi.2017 a female emerged (BVLS084).

BP: On 27.vi.2017 a larva of 13 mm was collected. On 1.vii.2017 the larva (15 mm) made a winter cocoon, and a male emerged in early February 2018 (BVLS089).

Conclusions

Based on the above observations, and the data in Table 2, our summarised results on the natural history of *Aprosthema tardum* are:

- The host plant is *Lathyrus latifolius*.

- Oviposition (see 2016 rearings and observations) is into the margin of a leaf, usually before these have unrolled. Eggs are usually laid singly, but two eggs are often laid in the same leaf margin, usually rather close together.

- Larvae feed on the leaves, at first only on the margins (Figs 15–17), while mature larvae consume the whole width of the leaf from the apex, leaving a characteristic "stepped" feeding trace (Fig. 8). They have been observed in the field from 23 April to 11 July (about 80 days). A larva requires only a single leaf to complete most of its feeding. There are five instars (four moults observed). A fully developed larva is 14–16 mm long.

- Most summer cocoons (Fig. 5), which are paler than winter cocoons, are loosely spun on a leaf of the host plant, exposed to the sun (Fig. 7), but some were made on other species of plants in the immediate vicinity of the host plant. Individual strands of silk are much thinner than in winter cocoons.

- Winter cocoons (Fig. 6), which are brownish in colour, are more tightly spun than summer cocoons, and made on the ground in the litter layer. Individual strands of silk are much thicker than in summer cocoons.

- Under rearing conditions, the egg stage lasts about 8 days, the larval stage about 16 days, and the cocoon stage of non-overwintering individuals (i.e. emerging in the same year) 10–14 days. For non-overwintering individuals, the complete duration of development is thus about 34–38 days.

- From eggs laid by overwintered females, possibly as early as March (see emergence dates No. 2, 3: Table 2), two generations complete their larval development during the same growing season. Existence of a partial third generation may be suggested by the late occurrence of summer cocoons (Table 2: 11, 12) and the emergence of a female, probably of the second generation, during the year in which it completed its immature stages (Table 2: 27). It is noteworthy that individuals with otherwise identical collection and rearing data, and which may even be siblings, did not always make the same type of cocoon (e.g. No. 18, 19: Table 2). Thus, a small number of individuals in the first generation, which normally form summer cocoons, seem instead to make winter cocoons and enter prolonged diapause, like almost all larvae of the second generation.

Discussion

Lorenz & Kraus (1957: 316) listed *Aprosthema tarda* [misspelling], without further comment, as associated with *Lathyrus*. As we mentioned in the introduction, the generally poor taxonomic understanding of *Aprosthema* has led to many misidentifications, and the indication of the host in Lorenz & Kraus (1957) needs substantiation. Vikberg (2004) suggested "? *Lathyrus sylvestris* L." to be a host of *A. tardum*, because one adult female of the summer generation was found in southern Finland on that plant. The statement in Zhelochovtsev (1988), that *Vicia* is a host of *A. tardum*, is thought to be a mistake resulting from misidentification of the sawfly species (Vikberg 2004). Although we concluded that *Lathyrus latifolius* is the main, or possibly only, host plant species in a part of south-west Europe, it is conceivable that *A. tardum* shows regional differences in which foodplant it uses. Vikberg's suggestion may point in this direction, or at least to possible oligophagy of *A. tardum* on *Lathyrus*. *Lathyrus latifolius* and *sylvestris* are closely related and very similar, but the latter has a more northern and upland distribution than the former (Hossaert-McKey & Jarry 1992). The phenomenon of regional changes in host plant choice is at present known to occur only in rather few sawfly species, but is quite likely to have been frequently overlooked, because data on the hosts of sawflies are generally incomplete, particularly in the more southern parts of Europe.

The development and behaviour of *A. tardum*, as recorded by us in southern France, is generally similar to that described by Vikberg (2004) in northern Europe for other species of the genus, although a few details seem to differ, or were not recorded in the latter study. It would, for example, be interesting to know if the first generation of larvae of northern populations of *A. tardum* contains individuals which enter prolonged (overwintering) diapause, as was found to be the case in southern France. A possible difference in the susceptibility of *A. tardum* larvae to attack by ants, correlated with the stage of development of the larva (see rearings and observations), suggests that investigation of interactions of larvae with ants might also be interesting. Finally, it is noteworthy that the feeding traces left by the young larvae of *A. tardum* are not of the zig-zag type recently described for larvae of two other genera of Sterictiphorinae, i.e. *Aproceros leucopoda* Takeuchi, 1939 (Blank et al. 2010) and some species of *Sterictiphora* (Eiseman 2015, calling the zig-zag traces "sinusoidal channels"). Vikberg (2004) stated, without further details, that the larva of *A. melanurum* is a leaf-edge feeder, and we presume that he, like us, did not observe zig-zag feeding by young *Aprosthema* larvae.

The behaviour of female *A. tardum* while ovipositing is especially interesting with regard to the use of the valvulae 3 of the ovipositor. In particular, the pressing of the inner valvulae faces against the leaf surface is noteworthy. We are not aware that such an extreme alteration in the position of the valvulae relative to each other has hitherto been observed in other sawflies. Very possibly linked to this behaviour is the dense array of small spines on the inner surface of the valvulae of *A. tardum* (Fig. 19). Similar structures are developed in other *Aprosthema* species, as well as many *Arge*, but apparently not in Palaearctic sawfly families other than Argidae. Although it is unclear whether the function of the spines is sensory, or mechanical (so that the valvulae do not slip across the plant tissue), or a combination of both, a primarily mechanical function might be inferred from the different positioning of the valvulae during the three phases of oviposition: During phase one the valvulae 3 grip the leaf so that the lances and lancets can be inserted in a controlled way in the leaf at a precise position, without sliding around, and during phase three the abdomen tip is similarly held stationary by the valvulae so that the egg can be placed in the pocket. The pocket itself is probably mostly cut during phase two, during which greater movement of the abdomen tip is required, and the valvulae therefore do not clasp the leaf.

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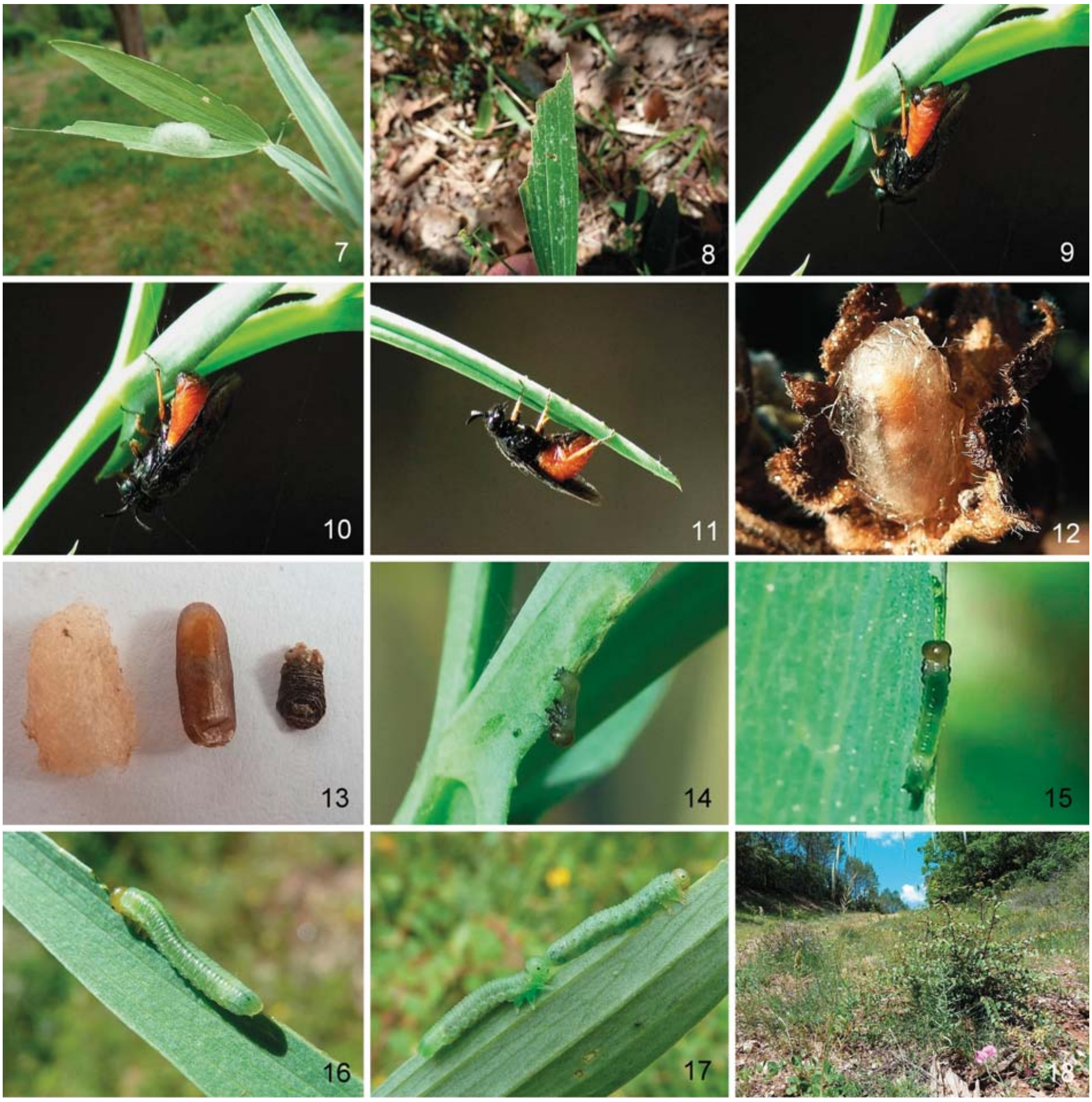
Figs 1–6: *Aprosthema tardum*. Head shape, dorsal view: **1**, summer morph, female (BVLS084). **2**, winter morph, female (BVLS040). **3**, summer morph, male (BVLS024). **4**, winter morph, male (BVLS039). For collection and rearing data, see Table 2. Cocoons: **5**, made by an individual emerging in the same summer (BVLS084). **6**, made by an overwintering individual (BVLS040).



Figs 7–18: *Aprosthema tardum*. **7**, empty summer cocoon (BVLS024) on leaf of host. **8**, typical "stepped" feeding trace made by larva. **9–11**, female (BVLS040) ovipositing in *Lathyrus latifolius*. **12**, winter cocoon (BVLS088) containing parasitoid cocoon. **13**, the same cocoon, cut open to reveal parasitoid cocoon and skin of host. **14–15**, instar 1 larva, length ca. 2 mm. **16**, instar 5 larva, length ca. 16 mm. **17**, two larvae on the same leaf, the one at left, with more uniform coloration, has recently moulted. **18**, Taradeau (TA), a typical habitat of *A. tardum* in the study area. At bottom right a *Lathyrus latifolius* plant (pink flower) is visible.

Fig. 19: *Aprosthema tardum*. Apex of sawsheath (valvulae 3), dorsal view (BVLS084). White arrows indicate spines on valvula inner surface. Inset: detail of spines.