Trifurcula pallidella (Duponchel, 1843) (Nepticulidae): distribution, biology and immature stages, particularly in Poland

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Abstract. *Trifurcula pallidella* (Duponchel, 1843) is recorded for the first time from 30 localities in south-eastern Poland. The biology is described and illustrated in detail for the first time: the larva makes spindle shaped galls in stems of *Chamaecytisus* spp., *Lembotropis nigricans*, and *Cytisus procumbens.* In Poland it is usually found on dry grassland or edges of woodland on calcareous soils. The larva, pupa and galls are described and illustrated. The distribution is revised and mapped on the basis of material and literature: its occurrence in Germany: Bavaria, Italy mainland and Sicily is confirmed, and new records are given for Corsica and Crete. It is widespread from Southeast Poland southwards throughout the Balkans and eastwards to the Volga, in the West to Regensburg in Germany, southern Switzerland, western Italy and Corsica. It is believed to use a different host in Mediterranean localities, possibly *Calicotome*. All known hosts and *Calicotome* belong to the monophyletic *Cytisus* group of recent molecular studies.

Zusammenfassung. *Trifurcula pallidella* (Duponchel, 1843) wird erstmals aus 30 Fundorten in Südostpolen gemeldet. Die Biologie wird zum ersten Mal detailliert beschrieben und abgebildet: die Raupe macht spindelförmige Galle im Stengel von *Chamaecytisus* spp., *Lembotropis nigricans*, und *Cytisus procumbens.* In Polen wird die Art meistens in Trockenrasen oder an Waldränder auf Kalkuntergrund gefunden. Die Raupe, Pupe und Galle werden beschrieben und abgebildet. Die Gesamtverbreitung wird auf Grund von Material und Literatur revidiert und auf einer Karte abgebildet: das Vorkommen in Deutschland: Bayern, auf dem Italienischen Festland und Sizilien wird bestätigt, und die Art wird von Korsika und Kreta neu nachgewiesen. *T. pallidella* ist weit verbreitet, von Südostpolen bis über die Balkanhalbinsel im Süden und nach Osten bis zur Wolga, im Westen bis Regensburg in Deutschland, die Südschweiz, Westitalien und Korsika. Es wird angenommen dass *T. pallidella* im Mittelmeerraum andere Futterpflanzen nutzt, wahrscheinlich *Calicotome*. Alle bekannten Futterpflanzen und *Calicotome* gehören zur monophyletische *Cytisus*-Gruppe die auch in rezenten molekularen Studien anerkannt wird.

Key words. *Trifurcula,* distribution maps, hostplants, galls, *Cytisus, Lembotropis, Chamaecytisus, Calicotome*, Fabaceae, Genisteae, Braconidae, *Mirax*.

Introduction

The genus *Trifurcula* Zeller, 1848 includes at least 36 named species in Europe (van Nieukerken 1996), particularly in the Mediterranean region, where also many unnamed species are known. More to the north the number of species is quickly decreasing, still sixteen species are found in the Czech Republic, eleven in Germany, seven in Denmark and five in Sweden. Only six species have been cited from Poland, which probably is an underestimate of the real number. The subgenus *Trifurcula* s. s. comprises a group of rather uniform moths, of which the larvae make stem-mines on Fabaceae (=Leguminosae). Two species groups are recognised: the *T. subnitidella* group which feeds on plants belonging to various Fabaceae tribes (i.e. *Lotus,*

Figs. 1-4. Habitats of *Trifurcula pallidella*. **1**–**2**. Poland, Podlasie: Stare Stulno, May 2003, grassland on a sand dune, hostplant *Chamaecytisus ruthenicus*. **3**. Poland, Lublin Upland: Brzeźno reserve, May 2003, calciphilous community at the margin of a marsh, hostplant *C. ruthenicus*. **4**. Slovakia, Plešivec, Slovenský Kras: Hôrka, October 1992, a dry calcareous hill with grassland, hostplant *C. hirsutus* (not visible on photograph). Photos M. Sielezniew (**1**–**3**), E.J. van Nieukerken (**4**).

Dorycnium, Coronilla), but not on brooms (tribe Genisteae), and the *T. pallidella* group, which is specialised on brooms.

The type species of *Trifurcula*, *T. pallidella* (Duponchel, 1843) is one of the largest species in the genus and one of the oldest known. Taxonomy and distribution were discussed by van Nieukerken & Johansson (1986), especially in relation to *T. beirnei* Puplesis, 1984, which previously had often been misidentified as *T. pallidella*. At that time the biology was unknown, although it was presumed that *T. pallidella* is associated with *Lembotropis nigricans* (L.) Griseb.

Shortly after that, the larvae were discovered by the senior author during a joint excursion with Aleš and Zdeněk Laštůvka. The larvae make galls in *Lembotropis nigricans* and *Chamaecytisus* spp. and later galls were also found in *Cytisus procumbens* (Waldst. & Kit. ex Willd.) Sprengel (=*Corothamnus procumbens*). The gall is shown and briefly described by A. & Z. Laštůvka (1997). The two Polish authors have found adults and galls of *Trifurcula pallidella* in several places in Poland since 1998. On the basis of these records the species was listed as occurring in Poland by Buszko & Nowacki (2000). We here report the Polish records in particular and provide details on the biology, immature stages and distribution in Poland and in Europe, where many new data have become available since 1986.

Material and methods

The first two Polish males of *T. pallidella* were found amongst material collected at light in xerothermic habitats in south-east Poland in 1998. In late autumn (20 October) of the same year, several empty galls were found in stems of *Lembotropis nigricans* and *Chamaecytisus ruthenicus* (Fischer ex Wołoszczak) A. Klásková in steppe vegetation in Machnów. The distribution of the host plants (Zając & Zając 2001) suggested that the species may have a wider range in Poland. Therefore we started detailed field investigations in 2001-2002 in order to test this hypothesis. A number of localities where the hostplants were expected were selected; these had similar biotic conditions as those mentioned above. Most of these sites are located in existing or planned nature reserves. We visited these sites from mid-September to mid-October: the period when the galls with larvae were expected. Some live material was also sent to the senior author, who reared a couple of specimens as well.

The senior author collected *T. pallidella* in the Czech and Slovak Republics in 1992 in collaboration with A. and Z. Laštůvka on localities were adults had been found previously. Other material studied was found during study of many museum and private collections since 1986, and some data were received from A. and Z. Laštůvka. He also re-examined all known literature citations.

Galls were collected by cutting parts of the stem of the hostplant. The stems were placed in plastic containers lined with tissue. Most larvae easily prepared cocoons on the tissue, after which the stems were removed and dried. Adults and parasites emerged after a winter diapause in an outhouse.

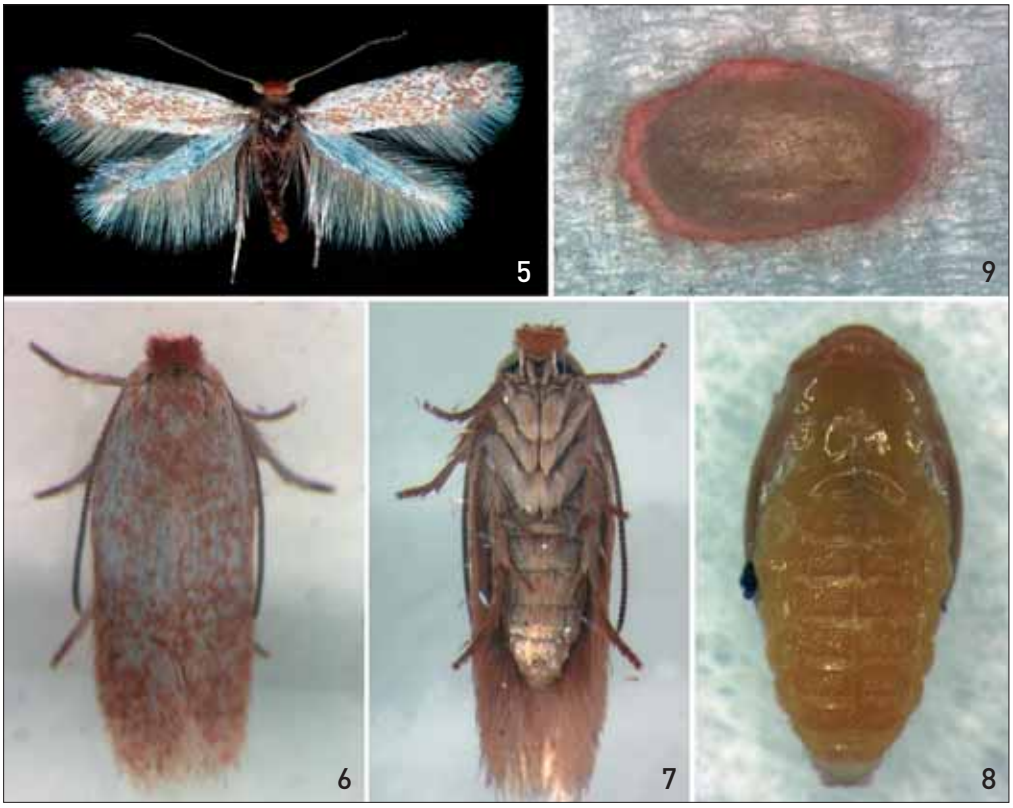
Larvae and pupal skins were examined after macerating in KOH and mounted on slides with euparal, after dehydration with ethanol and staining with chlorazol black and haemaluin. Galls were studied by simply cutting them with razor blades.

Morphological terms of larvae follow Gustafsson (1981), except for the naming of setae on the mesothorax, which follows Hoare (2000), in exchanging resp. the names of D1 and D2 and SV1 and SV2. Homologisation of setae, however, remains problematical. For this reason the ventral group of setae is not labelled in Fig. 21.

Photographs of preparations of immature stages and genitalia were taken with a Zeiss AxioCam digital camera attached to a Zeiss Axioskop H, those of live insects and galls by EvN with the same camera on Zeiss Stemi SV 11, using Carl Zeiss AxioVision 3.0.6 software. Galls were photographed by KP with a Canon D10 digital camera, with a standard lens. The adult moth was photographed with an Olympus DP10 digital camera attached to the stereo-microscope Olympus S260.

The European distribution map was prepared with Dmap 7.0 (Morton 2000). In Tab. 1 and 2 we give summarized locality data, all details of these, dates and UTM coordinates with an accuracy of 10 square kilometres are given in an excel sheet on the website of the senior author (http://www.naturalis.nl/nieukerken) and on the website of the journal (http://www.soceurlep.org/council-main.htm). When coordinates were not available from the source, we obtained most from NIMA (2004).

Depositories of collections are abbreviated according to Evenhuis & Samuelson (2004). For the hostplant names we follow Heywood & Ball (1968). Although since then there



Figs. 5–9. *Trifurcula pallidella.* **5.** Male, Poland: Stawska Góra res. **6–7.** Live female, Poland, Góry Pieprzowe res., emerged in Leiden. **8.** Live pupa, dorsal view, Poland, Stawska Góra res. **9.** Cocoon on tissue, Góry Pieprzowe res. Photos: J. Chobotow (**5**), E.J. van Nieukerken (**6–9**).

has been much discussion on the generic limits within the *Cytisus* group and the Genisteae in general, no consensus has been reached, and there is not another easy single source except the ILDIS database (ILDIS 2003), which uses a somewhat inconsistent nomenclature. The genera *Lembotropis* and *Chamaecytisus* as used here are often (but not always in the same paper) regarded as sections of *Cytisus* (resp. sect. *Lembotropis* and *Tubocytisus*), and the section *Corothamnus* in *Cytisus* (for *C. procumbens*) is in some publications raised to genus. In recent molecular studies, cited below, a large *Cytisus* seems to be paraphyletic, but also the genus *Chamaecytisus* as currently understood appears as polyphyletic (for a revision of this taxon see Cristofolini 1991).

RESULTS

Trifurcula pallidella (Duponchel)

Oecophora pallidella Duponchel, [1843]: 339, pl. 78. Lectotype selected by van Nieukerken & Johansson 1986.
Trifurcula pallidella; Zeller 1848: 332.
Trifurcula incognitella Toll 1936: 409.
Trifurcula pallidella; van Nieukerken & Johansson 1986: 271.

Diagnosis. Wingspan 7.5–9 mm. Head: frontal tuft from almost white, yellowish orange to brown ferruginous, collar white to straw, occasionally with a few darker scales. Scape straw to ferruginous orange, flagellum grey-ochreous indistinctly ringed, 42–50 segments. Thorax and forewings uniformly coloured, covered with two types of scales: white and ferruginous-tipped scales, sometimes with golden gloss. The ferruginous-tipped scales usually becoming more abundant towards apex. The general impression of the wing colour varies from white to ochreous, depending on abundance of scale type. Hindwing grey with straw cilia. Abdomen grey dorsally, straw ventrally.

Similar species. Of the species with which it can be found together, *Trifurcula pallidella* resembles *T. beirnei* most; this can in many cases be differentiated by the different flying period: *T. pallidella* occurs from May to early (mid) July, *T. beirnei* usually in August to September. However, there are a few earlier records of *T. beirnei*, thus July specimens need to be checked carefully. *T. beirnei* is on average larger (8–11 mm) than *T. pallidella*, and has three types of scales (white, yellow and dark tipped). The characteristic gnathos and large curved valvae of *T. beirnei* can often be seen without dissection.

Most other species likely to confuse with *T. pallidella* belong to the *T. immundella* complex of species, and of these *T. immundella* (Zeller, 1839) and *T. chamaecytisi* Z. & A. Laštůvka, 1994 resemble *T. pallidella* most, but larger and worn specimens of the other species may also be confused. Most of these species, except *T. immundella*, feed on the same hosts as *pallidella*, and can therefore be found in the same localities. These species are on average somewhat smaller (6–8.5 mm, sometimes even smaller), and apart from *T. chamaecytisi*, they are darker when fresh. In collections *T. pallidella* was often confused with the much smaller (5–7 mm) *T. serotinella* Herrich-Schäffer, 1855. The male genitalia offer the best characters, for descriptions and illustrations we refer to van Nieukerken & Johansson (1986), but we also illustrate here the male genitalia (Fig. 17).

Life history

Hostplants. With certainty galls are now recorded from *Chamaecytisus albus* (Hacq.) Rothm., *C. austriacus* (L.) Link, *C. hirsutus* (L.) Link, *C. ratisbonensis* (Schaeffer) Rothm., *C. ruthenicus* (Fischer ex Wołoszczak) A. Klásková, *Cytisus procumbens* (Waldst. & Kit. ex Willd.) Sprengel (in section *Corothamnus*) and *Lembotropis nigricans* (L.) Griseb.

Galls. The galls with full-grown larvae were found from 9 September to early November. Galls occurred at different heights in the stem, both in older shoots and younger shoots of the same year. Occasionally two or three galls were found in the same stem. Old galls remain visible and can still be found in the next spring, at least until June (see Tab. 1 and 2).

The egg is deposited on the stem where later the gall forms, usually difficult to see. The larva first bores into the parenchyma and then feeds in a spiral gallery around the stem, successively moving upwards, also partly boring in the central woody part of the stem (Figs. 10–16). The stem is thickened more or less considerably by the larval

Figs. 10–16. *Trifurcula pallidella*, biology, galls and details, **10–14.** *Chamaecytisus ruthenicus*, Korhynie (11: Osłowo), **10.** Three galls. **11–13.** Various sections. **14.** Exit hole, indicated by arrow. **15–16.** Galls in *Lembotropis nigricans,* Stawska Góra res. Photos E.J. van Nieukerken (**10–14**), K. Pałka. (**15, 16**).

activity. The diameter of the galls varies from 3.2–6.0 mm (depending on stem thickness) and the length from 13-26 mm (n=20). The frass is deposited in the gallery (Figs. 11–13), in a similar fashion as in stem-mines of related *Trifurcula* species, almost filling the gallery.

The full fed larva quits the gall through a slit in its upper part, usually close to a stem bud (Fig. 14). The pupation takes place in a typical Nepticulidae cocoon (Fig. 9). Cocoon length is 2.7–3.7 mm (mean 3.3 mm, n=20), width 1.8–2.5 mm (mean 2.1 mm, n=20). Its colour is pale brown to ferruginous brown. In captivity the cocoons were attached to the walls of the rearing tubes, to the surface of a stem or on pieces of paper tissue. After hibernation in outdoor temperature, the adults emerged from the middle of May to early June.

Voltinism. The moths fly in central Europe from 9 May to 19 July, most in May and June, in southern Greece and Crete they fly from 9 April to 17 May, but also 10 June in northern Greece. The species is clearly univoltine.

Parasites. We reared several parasites of the family Braconidae, all belonging to *Mirax rufilabris* Haliday, 1833 (det. C. van Achterberg, Leiden). They emerged in the

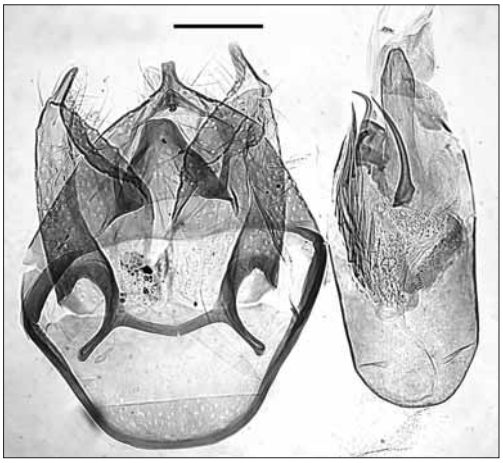


Fig. 17. *Trifurcula pallidella*, male genitalia, Germany: Kelheim, slide EJ7919. Scale 100µm.

laboratory between 9 April and 13 June 2003. We also reared just one specimen of Eulophidae, probably *Chrysocharis* sp. (5 June 2003). All these were reared out of the cocoons and thus both species are koinobionts. *Mirax rufilabris* has been recorded from many Nepticulidae species, including *Trifurcula immundella* (Shaw & Askew 1976), but it is now understood that *Mirax* forms a complex of several species with a narrower host range, of which a revision is in preparation (C. van Achterberg, pers. comm.).

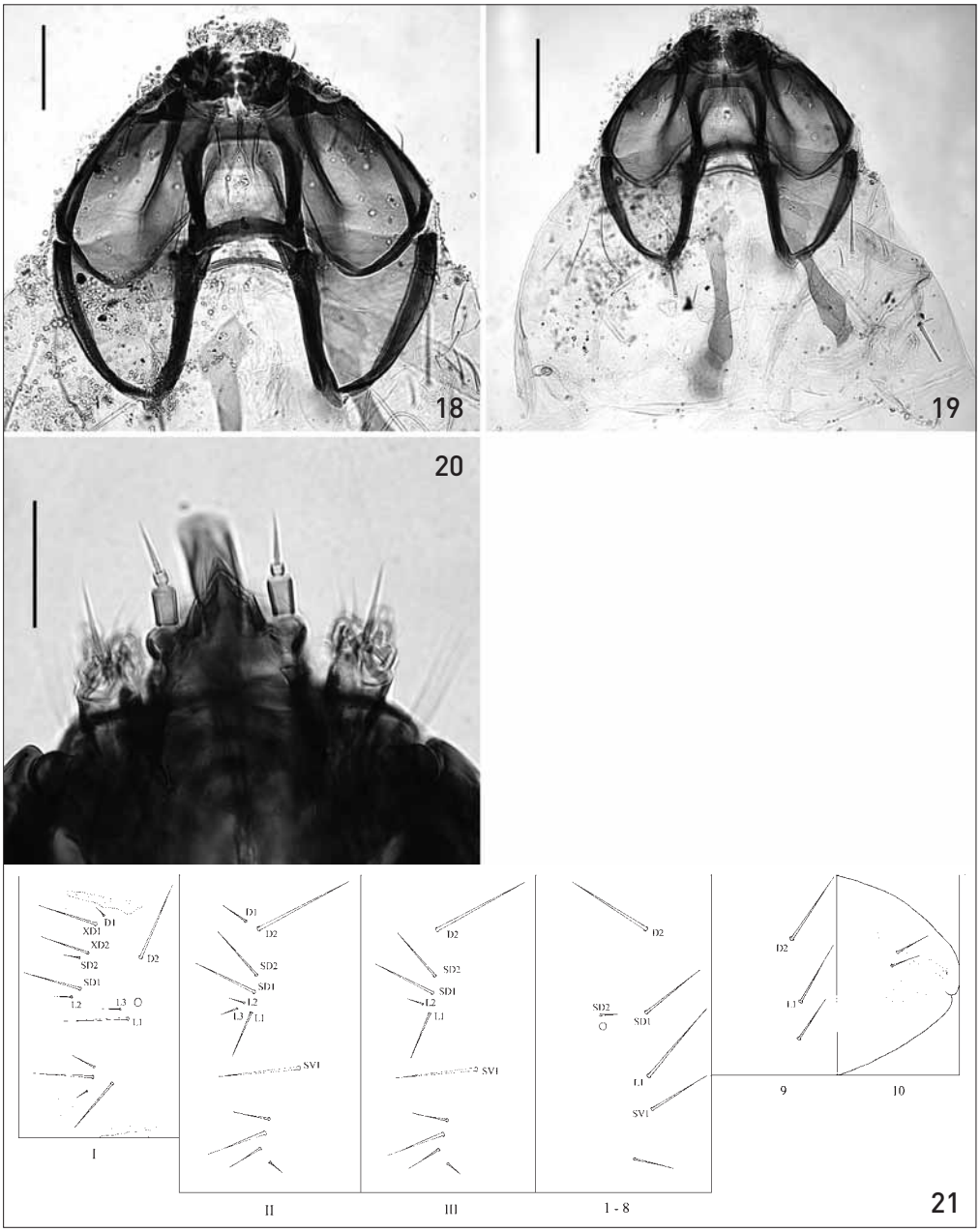
The type locality of *M. rufilabris* is Ireland, probably near Dublin. Haliday renamed it later *M. spartii*, an indication that he reared it from broom and thus from the only nepticulid known to feed on broom in Ireland: *T. immundella* (see Emmet 1976). According to C. van Achterberg, the 'real' *M. rufilabris* was up to now only known from *Trifurcula immundella*, and *T. pallidella* thus comprises a new host record. We may therefore assume that *M. rufilabris* is specialised on *Trifurcula* species that feed in the stem of brooms (see Tab. 1).

The rate of parasitism was high: from the material collected in autumn 2002 we reared 57 specimens of *Mirax*, one of *Chrysocharis* and only thirteen adults of *T. pallidella*.

Remarks. The galls were discovered by the senior author during joint field work with Aleš and Zdeněk Laštůvka in Vranovice, Moravia, 5 October 1992. In this locality adults were previously frequently caught around *Chamaecytisus ratisbonensis*. After failing to localise any stem-mines, he opened some spindle-shaped galls, and found to his surprise nepticulid larvae in it. Later several adults were reared from galls of various localities. These galls had also been noted and described before by Baudyš (1925) and Černik (1942), who found them in various localities in Moravia and Slovakia (Tab. 2). The larva was identified as 'unknown Microlepidopteron', and also cited in the handbook by Buhr (1964: 422) under *Cytisus* as number 2225. The galls are probably not induced by the egg-laying activity of the adult, but by the feeding larva; since it seems that the larva is not depending on tissue formed in the gall (but this needs to be checked more carefully). This type of thickening should not be called a gall according to some authors.

Description of immature stages

Larva (Figs. 18–21)**.** Mature larvae about 6–8 mm long, extremely slender, yellow when fresh. Body almost completely smooth, small spines (microtrichia) absent. Headcapsule 400–480 µm long, 440–515 µm wide (n=2), much wider than long. Labrum with 2 pairs of setae; mandibula with 4 strong cusps; labial palpus



Figs. 18–21. *Trifurcula pallidella*, larva, Stawska Góra res. **18.** Headcapsule, dorsal; scale 100µm. **19**. Headcapsule and prothorax, ventral; scale 200 µm. **20.** Detail of mouthparts, with labial palps; scale 50µm. **21.** Setal map, drawn by A. Mazurkiewicz & K. Pałka. Photos E.J. van Nieukerken.

with 3 segments and long terminal seta, second segment much longer than segment 1 or 3. Prothorax with pair of slender tergites and single indistinct sternite plus two small sternites anterolateral to the medial one; with the full complement of 13 pairs of

setae. Mesothorax with 12 pairs of setae (D1 present, 4 pairs of setae ventral to SV1), metathorax with 10 pairs (D1 and L3 absent). Abdominal segments 1-8 with 6 pairs, A9 with 3 pairs and A10 with 2 pairs. Distribution of setae illustrated in setal map (Fig. 21). Paired ventral ambulatory calli present on T2–3 and A1–7. Anal rods in A10 posteriorly bifid, forming an angle of almost 180°.

The larva differs from other described *Trifurcula* (s. str.) (Gustafsson 1981; Gustafsson & van Nieukerken 1990) by the large headcapsule, which is wider than long, the complete absence of microtrichia, the presence of D1 (named D2 by Gustafsson) on the mesothorax and the labial palpus which has a very long segment 2, but otherwise confirms with the generic description. Only *Trifurcula (Glaucolepis) headleyella* (Stainton, 1854) and *T. (T.) subnitidella* (Duponchel, 1843) have also 12 setal pairs on the mesothorax, the other studied Nepticulidae have only 11 (Gustafsson 1981; Gustafsson & van Nieukerken 1990; Hoare 2000). No setal map of a species of *Trifurcula* (s. str.) had been published previously.

Pupa (Figs. 8, 22–24). Pupal exuviae examined. Frons protruding slightly into conical projection, eyecaps large, at eclosion torn from frons. Abdominal tergites 2–8 covered with many spines, in about 3 to 5 rows per segment, but not arranged in distinct rows. Cremaster with two small hooks.

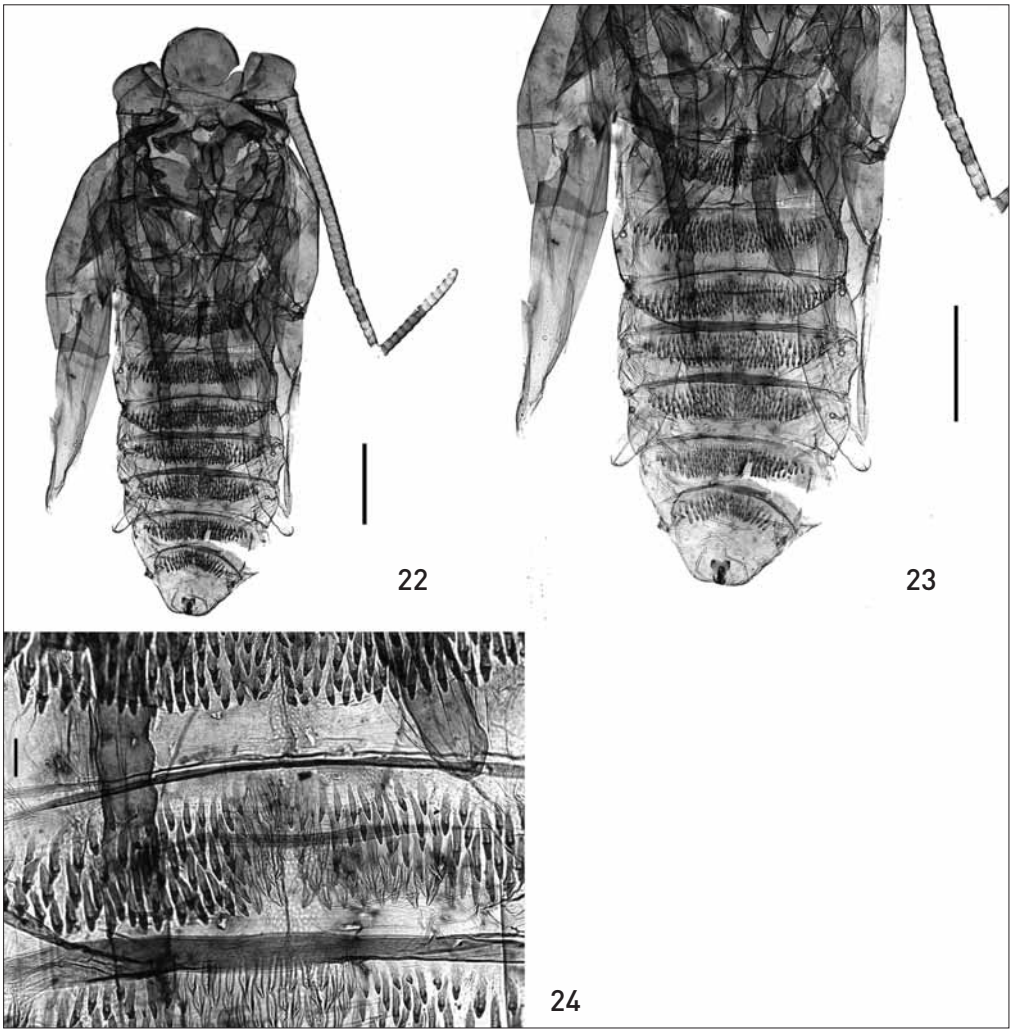
Distribution

Localities in Poland (Fig. 25). As a result of our studies, *T. pallidella* was found in 30 localities in south-east and east Poland. They are listed in Tab. 1 and presented on a map (Fig. 25).

The species reaches in Poland its northern distribution limits. The locality Grzybowce is the northernmost locality of this species in central Europe, but the Russian record in Ul'yanovsk Oblast is just a little further to the North.

European distribution (Fig. 26). In Tab. 2 we present all more or less reliable literature records and material seen by EvN or identified by colleagues sorted by country and locality. Since the previous revision of this species (van Nieukerken & Johansson 1986), many more data have become known, from which it appears that the previous suggestion that 'literature records can not be used at all' was too rigid. It is clear that the name *T. pallidella* was incorrectly used for *T. beirnei* in Great Britain, Denmark and parts of Germany and Poland. We have now also established that all previous records from France, Portugal and Spain are incorrect (van Nieukerken *et al.* 2004a, 2005): they are misidentifications for a number of pale *Trifurcula* species including *T. immundella*. From the overlapping part of the distributions of *T. pallidella* and *T. beirnei*, the records from Austria: Stelzing (Zeller in Krause 1871), Germany: Altenburg (Krause 1871; Borkowski 1975) and Poland: Sobótka (Zobten) (Wocke 1874; Puplesis 1984) definitely apply to *T. beirnei*. Two of the four localities on the Monte Baldo (Burmann & Huemer 1998), namely those in higher altitudes, refer to an unnamed species that is associated with *Genista radiata* (L.) Scop. (= *Cytisanthus radiatus*) (P. Huemer, *in litt.*) Other sources are reconsidered here in Tab. 2.

Many of the records presented in Tab. 2 are corroborated by either original material



Figs. 22–24. *Trifurcula pallidella*, pupal skin, dorsal view, Korhynie. Scales 500µm, 50µm (**24**). Photos: E.J. van Nieukerken.

or later findings. Others which have not been corroborated, are quite likely to be correct, but confirmation is still required (Italy: Pisa, Croatia, Macedonia, Rumania): they are all within the area where the known hosts occur and where the occurrence of *T. pallidella* is likely. Most problematic are records at the margin of the distribution area. The occurrence in Germany: Regensburg was previously doubted, and Segerer (1997) wrote: 'unüberprüfbare Angabe'. However, the occurrence in Germany is here corroborated by three specimens from three localities in Bavaria, including Regensburg (see Fig. 17). The record from Baden-Württemberg (Wörz 1958) has still to be rejected; it is a curious misidentification: upon checking, the specimen (coll. SMNS) appears to be a worn female of *Stigmella floslactella* (Haworth, 1828).

Fig. 25. Distribution of *Trifurcula pallidella* in Poland on 10km squares of the UTM grid.

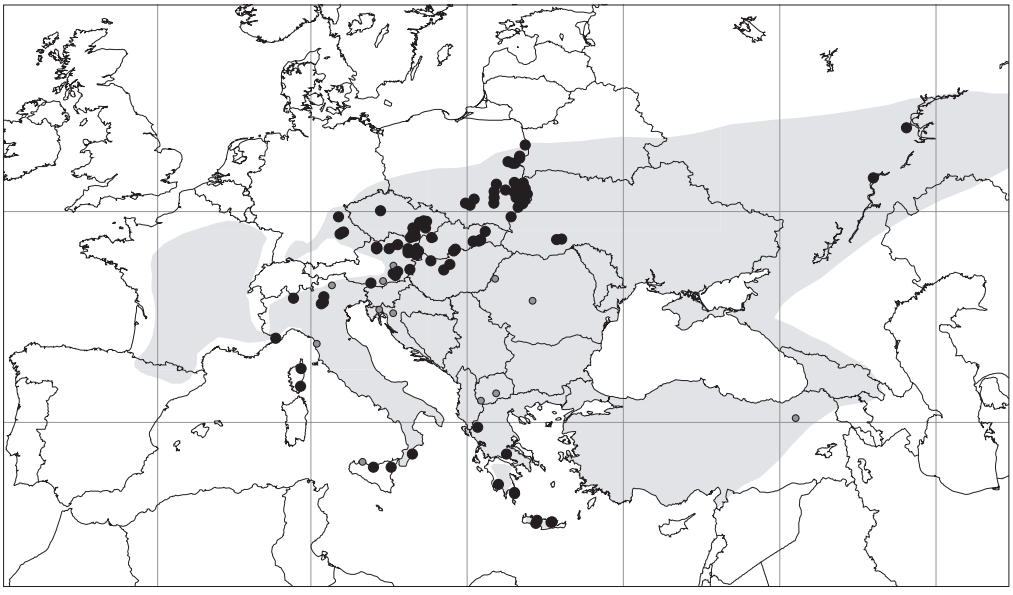


Fig. 26. Distribution of *Trifurcula pallidella*. Small grey circles: unconfirmed but not rejected literature records, large black circles: records confirmed by material, or reliable literature records. Grey shading gives the combined distribution of the hosts *Lembotropis nigricans* and *Chamaecytisus* spp. of the series *Tubocytisus* s. str. (Cristofolini 1991).

Tab. 1. Localities of *Trifurcula pallidella* in Poland and rearing results. UTM coordinates given as 10km squares, all in zone 34U. Hostplants: *Ca = Chamaecytisus albus*, *Cra. = C. ratisbonensis*, *Cru = C. ruthenicus*, *Ln= Lembotropis nigricans*. Other abbreviations: Chr. = *Chrysocharis* sp. (parasite), M = *Mirax rufilabris* (parasite), * = material sent to and reared in Leiden (in coll. RMNH). All material collected by A. Mazurkiewicz and / or K. Pałka.

Region	Locality	UTM	Habitat	Host	Stage	Date	reared
Lublin Upland	Brzeźno village	FB96	xerothermic rail-way embankment	*Cru*	old galls	8.v.2004	
	Brzeźno res.	FB87	edge of calcareous peat-bog	*Cru*	larvae	5.x.2002	3♂, 3♀, 5 M
					old galls	28.v.2004	
	Czumów	GB03	grassland on loess	*Cru*.	galls	15.x.2001	
	Gródek	GB03	grassland on loess	*Ca*	galls	11.xi.2004	
	Podzamcze res.	FB05	grassland on limestone rocks	*Cru*, *LN*	galls	7.x.2001	
				Cru	larvae	5.x.2002	2♀, 1 M
					1♂, 1♀	24-28.v.2004	
	Rogów res.	FB73	grassland on limestone rocks		1♂,1♀	25.v.2004	
	Skarpa Dobrska res.	EB68	grassland on loess		1♂	12.vi.1997	
				Cru, *LN*	galls	7.x.2001	
	Skarpa Dobużańska res.	FB90	grassland on loess	*Cru*	galls	15.x.2001	
	Stawska Góra res.	FB67	grassland on limestone rocks	*LN*	larvae	6.x.2001	2♂, 2♀
					larvae	3.x.2002	1♂, 21 M*
					larvae	10.x.2002	2♂, 5 M
	Tarnogóra	FB44	grassland on loess	*Cru*	galls	8.x.2000	
	Zalesie Kraszeńskie	FB57	xerothermic rail-way emb.	*Cru*	old galls	13.v.2004	
Małopolska Upland	Biała Góra res.	DA28	grassland on limestone rocks	*Cru*	galls	3.xi.2001	
	Biedrzychów	EB54	grassland on loess	*LN*	galls	2.x.2001	
	Góry Pieprzowe res.	EB51	grassland on loess		1♂	29.v.1995	
					2♂	2.vi.2001	
				Cru	larvae	3.x.2002	1♂, 1♀, 1 Chr, 6 M*
	Pińczów	DB60	grassland on gypsum	*LN*	galls	4.xi.2001	
					galls	10.x.2004	
	Wały res.	DA47	grassland on limestone rocks	*Cru*	galls	3.xi.2001	
Podlasie	Ciesacin res.	FB49	neutral grassland on sand on the edge of peat-bog	*Cru*	old galls	9.v.2004	
	Dobrowoda	FD62	grassland on gravel	*Cra*	galls	2.x.2002	*
	Drohiczyn	FD10	grassland on gravel	*Cru*	galls	2.x.2002	*
	Grzybowce	FD89	grassland on gravel	*Cru*	galls	9.x.2004	
	Mielnik – Przedmieście	FC49	grassland on gravel	*Cru*	galls	7.x.2001	
	Osłowo	FC39	grassland on gravel	*Cru*	galls	2.x.2002	9 M*
	Stare Stulno	FB89	neutral grassland on sand	*Cru*	galls	6.x.2001	
	Witowo, in Białowieża Primeval Forest	FD63	grassland on gravel	*Cru*	galls	2.x.2002	*
	Zagórze	FC39	grassland on gravel	*Cru*	galls	7.x.2001	
Roztocze	Biała Góra	FA79	grassland on limestone rocks	*Cru*, *LN*	galls	15.x.2001	
	Kąty II	FB51	grassland on limestone rocks	*Cru*, *LN*	galls	8.x.2000	
	Korhynie	FA88	grassland on limestone rocks	*Cru*, *LN*	galls	14.x.2001	
					galls	3.x.2002	4 M*
	Machnów	FA88	grassland on limestone rocks	*Cru*, *LN*	galls	20.x.1998	
					galls	25.ix.2004	
	Radruż	FA66	grassland on limestone rocks	*Cru*	larva	24.ix.2004	
Sandomierz Lowland	Nowa Dęba	EA58	neutral grassland on sand		1♂	3.vi.1998	
				Cru	galls	2.x.2001	
Przemyśl Hills	Złota Góra	FA31	grassland on gravel	*Cru*	galls	1.x.2001	

Tab. 2. Records of *Trifurcula pallidella*, except for Poland. The countries are indicated by their ISO codes, and some provinces abbreviated. Hostplants: *Ca* = *Chamaecytisus austriacus*, *Ch* = *C. hirsutus*, *Cr* = *C. ratisbonensis*, *Ln*= *Lembotropis nigricans*. Abbreviations: AZL = A. & Z. Laštůvka, EvN = E. van Nieukerken. Collection codons follow Evenhuis & Samuelson (2004). Reliability: ! after collectioncodon: material seen by EvN; ? not impossible, fits in distribution and biology, but confirmation required, ?? questionable (but not completely rejected). The remaining literature references are either reliable (genitalia check, recent authors, galls or circumstantial evidence) or at least likely records.
Key to sources: 1. Anikin 2001, 2. Baudyš 1925, 3. Baudyš 1931, 4. Baudyš 1947, 5. Burmann & Huemer 1998, 6. Caradja 1899, 7. Caradja 1901, 8. Černik 1942, 9. Curó 1883, 10. Czekelius 1924, 11. Hartig 1964, 12. Hauder 1912, 13. Hauder 1924, 14. Herrich-Schäffer 1847-1855, 15. Hrubý 1964, 16. Issekutz 1972, 17. Kasy 1985, 18. Klimesch 1949, 19. Klimesch 1961, 20. Klimesch 1968, 21. Klimesch 1990, 22. Laštůvka 1994, 23. Z. & A. Laštůvka 1994, 24. A. & Z. Laštůvka in litt., 25. Mann 1862, 26. Mann 1866, 27. Mann 1869, 28. Mann 1885, 29. Mariani 1938, 30. Mariani 1943, 31. Müller-Rutz 1922, 32. Nickerl 1908, 33. van Nieukerken & Johansson 1986, 34. van Nieukerken et al. 2004, 35. Pável & Uhryk 1896, 36. Prohaska & Hoffmann 1929, 37. Pröse & Segerer 1999, 38. Puplesis 1994, 39. Rebel 1899, 40. Schmid 1886, 41. Skala 1933, 42. Szőcs 1965, 43. Tokár et al. 1999, 44. Toll 1936, 45. Toll 1938, 46. Vorbrodt 1932, 47. Zeller 1850, 48. Zimmermann 1944b, 49. Zimmermann 1944a.

Country, Locality		**collector**	**stage, host**	**Source**
AT: BU	Bruck an der Leitha, Spitalberg	Preissecker	1♂	19, 49, NMW!
	Rechnitz, Donatikapella	Koschabek	1♂	16, 19
	Schieferberg, Leithagebirge	Kasy	1♂	33, NMW!
AT: KÄ	Villach	Preissecker	1♀	NHMB!
AT: NÖ	Fürbachwiesen, Gramatneusiedl	Kasy	4♂	17, 33, NMW!, RMNH!
	Hundsheimer Berg	Kasy	1♂	33, NMW!
	Jauerling	Preissecker		49
	Mödling [Goldene Stiege]		1♂	HNHM!
	Oberweiden	Preissecker		49
	Ostrong [Klimesch Haide]	Preissecker	1♂	21, 49, NMW!
	Pfaffstätten		1♀	HNHM!
	Stein a. D., Goldburg	Preissecker	1♂	49, NMW!
	Ysper	Preissecker	1♂	49, NMW!
AT: OÖ	Berg (Alpenvorland)	Wolfschläger		12, 21, 41
	Bergham	Wolfschläger		13, 41
	Diessenleiten	Hauder		13, 21, 41
	Ebelsberg (Alpenvorland)	Klimesch	[1♀!]	21, ZSM!
	Koglerau, Waldblösse	Knitschke	1♂	12, 21, 41, NMW!
	Linz, Linz kgl. [Koglerau]	Hauder	3♂	NHMB!, ZFMK!
	Linz-Uhrfahrwänd	Klimesch	[1♂!]	18, 21, ZSM!
AT: ST	Bruck a. Mur	Klimesch		19
	Graz; Graz, Plabutsch		9♂	33, 36, HNHM!, NHMB!, NHRS!, NMW!
	Premstätten	Prohaska	1♂	36, HNHM!
	Weiz	Knitschke	2♂	NMW!
AT: WI	Wien	Mann	4♂	14, 33, MNHN (LT)!, BMNH!
	Laaerberger Remisen	Mann		28, 49
	Mauer	Mann	1♀	19, 28, 49, NMW!
	Rodaun	Mann		19, 28, 49
	Tivoli	Mann		28, 49
	Wien, Dornbach		1♂	NMW!
CH	Ticino: Maroggia	Krüger	1♂	31, 46, NHMB!
CZ: Boh	Praha (Prag-Krtsch)	Nickerl		23, 32, 48

Country, Locality		collector	stage, host	Source
CZ:Mor.	Brno		gall, *Ln*	2
	Bulhary	AZL	larvae, *Ca*	22, 23
	Čelechovice na Hané	AZL		23, AZL!
	Dětkovice	AZL	15♂	23, RMNH!
	Dolní Dunajovice	AZL	larvae, *Ca*	23
	Hrušovany nad Jevišovkou	AZL	larvae, *Ca*	23
	Kvasice, Kvasická skála rock	Zavřel	gall, *Cr*	4
	Mikulov, Stráně u Sedlece	Picbauer, AZL	gall, *Ca*	4, 22,
	Mikulov, Pavlovské vrchy, Stolová h.	EvN	gall *Ca*	RMNH!
	Myslejovice	AZL	1♂	23, AZL!
	Olomouc, Neboteiner Berg	Černik	*Cr, Ln*	8
	Pouzdřany	Picbauer	gall, *Ln*	2
	Tuřany		gall, *Ln*	2
	Vicov	AZL	1♂	23
	Vranovice	AZL, EvN	7♂, 2♀, e.l. *Cr*	23, RMNH!
DE: BA	Grafenwöhr	Klimesch	1♂	ZSM!
	Kelheim Donau: Auf der Brand	E. Jäckh	1♂	USNM!
	Regensburg [Tegernheimerberge]		1♂	14, 37, 40, ETHZ!
FR– 2A	St. Lucia di Porto Vecchio	Liška	1♂	24
FR- 2B	15 km S. Bastia	Karsholt	1♂	24, ZMUC
GR–CR	Irakleio: Potamies	Johansson	2♂	RMNH!, Johansson!
	Irakleio: Stalis, Chersonisos	Bengtsson	2♂	Bengtsson!
	Rethymno: Plakias	Johansson	1♂	Johansson!
	Rethymno	Johansson	1§	Johansson!
GR	Fthiotis: Delfoi	Selling	1♂, 1♀	ZMUC!
	Ioannina: Asprángeli	AZL	2♂	24
	Lakonia: 5 km S Monemvasia	Skule,Christ.	1♂, 1♀	33, ZMUC!
	Lakonia: 7 km SW Monemvasia	Skule	1♂	33, ZMUC!
	Messinia: Messini	Horak	1♂	33, ZMUC!
HR	Josipdol			35?
	Rijeka (Fiume) (Istria)			30, 35?
	Dalmatia [no detail]			27?
HU	Budakeszi, Hársbokorhegy			42
	Nadap	Gozmany	1♂	42, HNHM!
	Nyír, Kecskemét	Klimesch	1♂	ZSM!
IT	Bolzano	Hedemann		11, 30, 39
	Bolzano: Renon: Collalbo	Hartig	1♂	11
	Catanzaro: Sta Catarina dello Ionio	AZL	1♀	24
	Imperia: Pieve d.T., Monesi	Liška	2♂	24
	Pisa	Mann		9, 14, 30, 47
	Trento: Pietramurata nei boschi	Jäckh	1♂	photograph in RMNH! [USNM]
	Verona: Mte Baldo, Ferrara + Pai	Burmann		5
IT-SIC	Messina: Francavilla di Sicilia	AZL	1♀	24
	Palermo: Castelbuono	AZL	1♂	24
	Palermitano (Sicilia)	Mann		9, 30
	Palermo: Vallecorta			29
	Palermo: San Martino delle Scale	Klimesch	3♂, 1♀	ZSM!
MK	Drenovo-Kav.	Klimesch		20
RO	Sibiu (as Hermannstadt)	Prall		10?
	Tulcea (as Tultscha)	Mann		6, 7?, 26
RU	Saratov	Anikin		1, 38
	Ul'yanovsk: Srednikovo, Povolzhye	Zolotuhin	1♂	34, coll. Zolotuhin!
SI	Carniola	Mann		9?
SK	Čebovce	AZL	2♂	23, AZL!
	Kočovce (Kocsócz)			15, 23?, 35
	Nové Mesto nad Váhom	Patočka		15, 23
	Plešivec	AZL, Patočka	1♂, *Ch*	23, 43
	Plešivec, Slov. Kras.: Hôrka	EvN	2♂, 2♀ e.l., *Ch*	RMNH!
	Velký Šariš, Prešov	Suza	gall, *Ca*	3
	Zádiel, Slovensky Kras	AZL, EvN	3♂, 1♀, el *Ln*	23, AZL!, RMNH!
TR	Bursa (Brussa)	Mann		25??
UA	Borshchiv area, S: Babuchow	Toll		44, 45
	Zalishchyky area: Obizowa	Toll		44, 45

The old record from Turkey (Mann 1862) is questionable: in Turkey occurs also a large pale species of *Trifurcula (Glaucolepis)*, which could easily be confused, but the occurrence of *T. pallidella* in Turkey is also to be expected.
The record of *T. pallidella* in September by Schmid (1886) is probably a misidentification for *T. beirnei*, likewise the August record from Macedonia (Klimesch 1968) is not accepted, but in both cases earlier records in the same area are considered as possibly correct *pallidella*. The record from 'Alpi Marittimi' (Mariani 1943) may refer to the incorrect record from the French department Alpes Maritimes (Cannes), but the recent record from Mónesi in the Alpi Marittimi very close to the French border also confirms its occurrence here in Italy. This also makes it more likely that real *T. pallidella* can after all be found in the French Department Alpes Maritimes.
In summary, *T. pallidella* is distributed from Southeast Germany (Bayern), east into Bohemia, Moravia, Slovakia, adjacent SE Poland, much of Austria, both along the Danube and East and South of the Alps, extending through the Balkans (with very few verified records) to southern Greece (Peloponnesus) and Crete, eastwards through Ukraine and Russia to the Volga, and one questionable record from Turkey. To the West it occurs in northern Italy almost reaching France, just extending into Switzerland (Ticino), and throughout Italy to Sicily and Corsica.
Habitats. In Poland and Slovakia the species was found in warm and dry grasslands or open woodland, often on calcareous soils, but also on sand or gravel (Figs. 1, 2, 4, Tab. 1). In one case (Brzeźno reserve, Fig. 3) it was found in a relatively wet habitat on the edge of a calcareous bog. Elsewhere in Europe it occurs in a variety of habitats, although usually on relatively warm places: often sunny slopes in river valleys, such as that of the Danube in Germany, Austria and Hungary. The hosts are frequently associated with *Quercus pubescens* woodland. The localities in Corsica, Greece and Crete are Mediterranean shrubland (garrigue, maquis or phrygana), often close to the sea. The altitudinal range is from sea level to 1000 m, with one record at 1600 m in Italy (Imperia, Monesi, Alpi Marittimi).
In 2001 and 2002 the species was extremely abundant in Poland, and larvae could be found in large numbers in most places. In contrast to that, in October 2004 almost no larvae or galls could be found in several of the same localities. Most localities in Central Europe are in Nature reserves, and the species may be vulnerable to increasing pressure by agricultural development and manure.

Discussion

Distribution and hostplant relationships. *Trifurcula pallidella* occurs commonly in many parts of the distribution area of its presumed hosts and is much more common than previously assumed (van Nieukerken & Johansson 1986). However, it has as yet not been found in the more western part of the distribution area of species of *Chamaecytisus*, e.g. France, parts of Germany and Spain. On the other hand, the distribution of *T. pallidella* cannot be explained completely by the distribution of the known hosts in the southern part of its range: no species of *Lembotropis, Chamaecytisus* or *Cytisus* sect. *Corothamnus* are known from Corsica or Sicily, and

the relatively common occurrence of *T. pallidella* in southern Greece and Crete, contrasts with the sparse occurrence of just a few species of *Chamaecytisus*. In fact in this part of Greece and Crete only three species of brooms are frequent: *Calicotome villosa* (Poiret) Link, *Spartium junceum* L. and *Genista acanthoclada* DC. (Turland *et al.* 1993, EvN, personal observation in Peloponnesus).

Recent studies on the molecular phylogeny of the Genisteae (Cubas *et al.* 2002) support at least two large monophyletic clades: a *Genista* group and a *Cytisus* group. Käss & Wink (1995; 1997) find support for a division of the *Cytisus* groups in two clades using rbcL sequences and Neighbour Joining, in which *Chamaecytisus* is polyphyletic and dispersed over both clades, but all hostplants of *T. pallidella* in the analysis, group together with *Cytisus multiflorus*, *C. arboreus* and *Calicotome villosa*. However, in the ITS sequence and in MP analyses of both genes (Käss & Wink 1997), a monophyletic *Cytisus* group including *Calicotome* is supported. These authors therefore suggest to synonymise the genera *Lembotropis, Chamaecytisus* and *Calicotome* with *Cytisus.* Combining these results with the previous observations leads to the hypothesis that in the Mediterranean region *Calicotome* is a very likely alternative hostplant for *T. pallidella*, and that *T. pallidella* is specialised on a number of species (but not all) within the *Cytisus* clade.

There is an interesting parallel with the *Trifurcula immundella* species complex: this is a group of very closely related species, which feed on about the same hosts as *T. pallidella*, but the species in this complex are almost strictly monophagous: each feeds on only one or a few related hosts: *T. immundella* feeds on *Cytisus scoparius* (L.) Link, *T. moravica* Z. & A. Laštůvka, 1994 on *Lembotropis nigricans, T. corothamni* Z. & A. Laštůvka, 1994 on *C. procumbens¸ T. chamaecytisi* on *Chamaecytisus* and *T. calycotomella* A. & Z. & Laštůvka, 1997 on *Calicotome* spp. (Z. & A. Laštůvka 1994): all feeding on the *Cytisus* group and these species – apart from *T. immundella* – have combined the same host range as *T. pallidella*.

Galling. *Trifurcula pallidella* is the only species of the genus causing galls, the other species of the subgenus *Trifurcula* exclusively making stem-mines (van Nieukerken 1990; Z. & A. Laštůvka 1994; A. & Z. Laštůvka 1997), and most representatives of the other subgenera (*Levarchama* and *Glaucolepis*) make leafmines, a few *Glaucolepis* also stem-mines. The galls of *T. pallidella* in a way resemble the stem-mines, but the larva seems to feed in deeper tissue than is usual for *Trifurcula* (s. str.) species. It places *T. pallidella* in a rather isolated position in the genus, and also morphologically it is not very close to any other species. There is no apparent explanation why this species changed the stemmining habit into galling: on the same hostplants stem-mining species also occur as discussed above, so the plant itself cannot be the reason. The larva does not show special adaptations to the galling habit, it is only larger than most other Nepticulidae larvae, and the mandibular cusps are relatively strongly developed.

Galling has originated several times independently in the Nepticulidae: there are at least three other examples. The North American type species of the genus *Ectoedemia* (which means as much as an external swelling), *Ectoedemia populella* Busck, 1907 is causing globular galls in the petiole of *Populus* (Busck 1907). Related species in the

populella species group also cause thickened petioles by their feeding habit, but these are not considered real galls. Most likely *E. populella* evolved from a petiole mining species. *Ectoedemia (Zimmermannia) castaneae* Busck, 1913, another North-American species, makes galls on bark of *Castanea* (Busck 1913), and probably evolved from barkmining species. Further *Ectoedemia (Fomoria) nigrifasciata* (Walsingham, 1908) from the Canary Islands makes a combined gall and mine in the Apocynaceae *Periploca laevigata* Ait. (Klimesch 1972); its closest relatives are leafmining on *Euphorbia*.

For two species of *Trifurcula* the larval way of feeding is still unknown: *T. beirnei* and *T. squamatella* Stainton, 1849. Both are relatively large species (the largest in the genus), associated with resp. *Genista* species and *Cytisus scoparius*. It is well worth considering the possibility that they are also gall makers, when searching for their larvae.

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