BIOSYSTEMATICS OF INSECTS LIVING IN FEMALE BIRCH CATKINS. IV. EGG-LARVAL PARASITOIDS OF THE GENERA *PLATYGASTER* LATREILLE AND *METACLISIS* FÖRSTER (HYMENOPTERA, PLATYGASTRIDAE)

by

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ABSTRACT

Adult and larval stages of *Platygaster betularia* Kieffer, *P. betulae* (Kieffer) and *Metaclisis phragmitis* Debauche are described. These species are egg-larval parasitoids of three gall midge species, which belong to the genus *Semudobia* Kieffer (Diptera, Cecidomyiidae), in fruit catkins of *Betula* (Betulaceae). The various developmental stages of the *Platygaster* species are discriminated with the help of multivariate methods. Phenology, host specificity and effects upon host density have been investigated. All platygastrid parasitoids develop highly synchronized with their hosts. *Platygaster betularia* and *P. betulae* have mutually exclusive host preferences. Both *Platygaster* species are important mortality factors particularly able to eliminate moderate host densities. Speciation patterns in *Semudobia* and *Platygaster* have no parallel traits and can, therefore, not be regarded as results of a co-evolutionary process. Some notes are included about platygastrid parasitoids of Nearctic *Semudobia* species and of inquiline *Dasineura* gall midges in birch catkins.

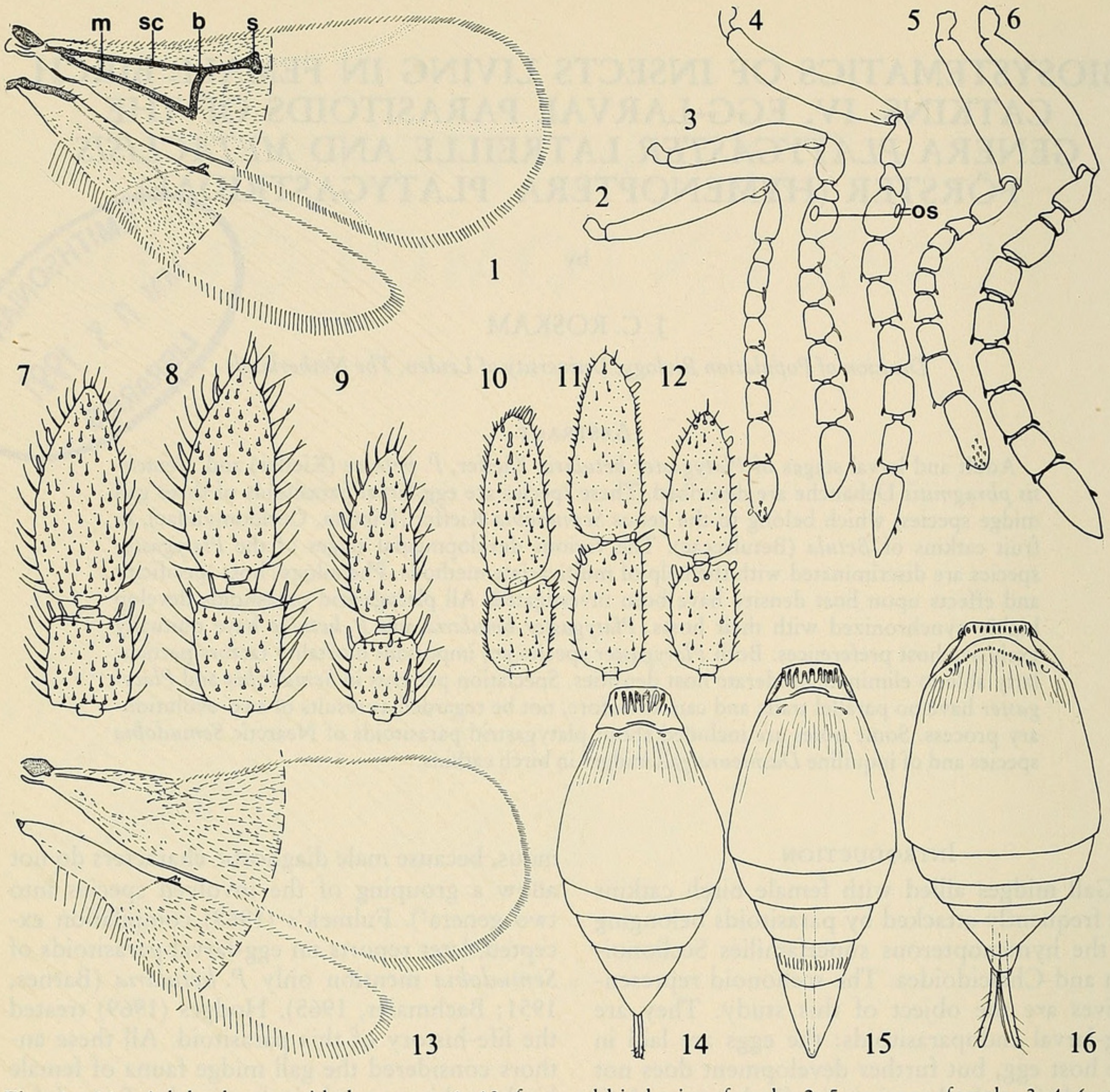
INTRODUCTION

Gall midges allied with female birch catkins are frequently attacked by parasitoids belonging to the hymenopterous superfamilies Scelionoidea and Chalcidoidea. The scelionoid representatives are the object of this study. They are egg-larval endoparasitoids: the eggs are laid in the host egg, but further development does not occur before the host is in its final instar. Until then parasitized hosts can not be distinguished from healthy ones. Parasitized early final instar hosts become inert and further development eventually ceases. One, or sometimes two larvae are visible inside the host, consuming all of the host's body contents within a few days. The skin of the host larva remains as a "cocoon", providing an extra protection for the mature parasitoid larva, in which it pupates.

Kieffer (1916) described two platygastrid parasitoids of *Semudobia betulae* (Winnertz) s.l., viz., *Platygaster betularia* Kieffer and *Misocyclops betulae* Kieffer. According to current opinion, also adopted in this paper, *Platygaster* Latreille and *Misocyclops* Kieffer are synonymous, because male diagnostic characters do not allow a grouping of the involved species into two genera[1]). Fulmek's (1968) compilation excepted, later reports on egg-larval parasitoids of *Semudobia* mention only *P. betularia* (Barnes, 1951; Bachmaier, 1965). Hodges (1969) treated the life-history of this parasitoid. All these authors considered the gall midge fauna of female birch catkins as relatively simple: *Semudobia betulae*, the gall maker, is accompanied by a saprophagous and a predaceous gall midge species, viz., *Clinodiplosis cilicrus* (Kieffer) and *Lestodiplosis* cf. *vorax* (Rübsaamen), respectively. Roskam (1977, 1979) and Roskam & van Uffelen (1981), however, arrived at the conclusion that at least five gall inducing *Semudobia* species and two inquiline *Dasineura* species are specialized on female birch catkins. *Clinodiplosis cilicrus* and *Lestodiplosis* cf. *vorax* are frequently present in this biocoenosis. The advancement of knowledge at the gall midge level provided a basis for further research of the parasitoids and the results of this study are now presented for the egg-larval parasitoids.

Platygaster betularia and *P. betulae* are both abundant in the Palaearctic entomofauna of female birch catkins. Among other things they are

[1]) A formal synonymy will be proposed by Mr. H. J. Vlug, Wageningen (pers. comm.).



Figs. 1—16. Adult platygastrid characters. 1, 13, fore and hind wing, female; 2, 5, antenna, female; 3, 4, 6, antenna, male; 7—9, ultimate and penultimate antennal segments, male; 10—12, ditto, female; 14—16, gaster, female. 1, 5—7, 10, 16, *Metaclisis phragmitis*; 2, 3, 9, 12—14. *Platygaster betularia*; 4, 8, 11, 15, *P. betulae*. b, basal vein; m, medial vein; os, oval sensilla; s, stigma; sc, subcostal vein. 1, 13—16, × 60; 2—6, × 96; 7—12, × 240.

characterized by different host associations: *P. betularia* has only been reared from *S. betulae* (Winnertz) s.s. and *S. skuhravae* Roskam, whereas *P. betulae* is restricted to *S. tarda* Roskam. *Metaclisis phragmitis* Debauche has been reared from both *S. betulae* and *S. tarda*. Also the Nearctic gall midge *S. brevipalpis* Roskam is attacked by a platygastrid: mature larvae have been found in one collection. These larvae are very aberrant in shape and belong to an undescribed genus.

Dasineura species have other platygastrid parasitoids. Because mature *Dasineura* larvae drop to the ground for hibernation, it was not possible to rear parasitoid full grown larvae and adults from these inquilines. However, in *Dasineura* larvae two different forms of platygastrid larvae have been observed: the first putatively belongs to *Piestopleura* cf. *mamertes* (Walker), the second could not be combined with adult platygastrids frequenting female birch catkins. No platygastrid parasitoids have been found in *Clinodiplosis* and *Lestodiplosis* larvae.

Material and methods

Immature stages. — Galls of different *Semudobia* species have different shapes and can therefore be sorted according to the gall inducing midge species (Roskam, 1977). In order to detect the parasitoids, the host larvae were dissected from identified galls and macerated in warm 80% lactic acid. Platygastrid larvae were taken from opened hosts and slide-mounted in polyvinyl-lactophenol. Galls were also collected from dry herbarium material. Then 10% KOH was used for maceration.

Adults. — Adults were collected by rearing them from samples of identified galls, and by collecting ovipositing females from female catkins with an exhauster. This material was either stored in 80% ethanol, or mounted on tags, or dissected and slide-mounted in euparal. Specimens representing all stages of the studied species have been deposited in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden.

Phenological observations on immature stages were made by analyzing samples of ten fruit catkins each. The samples were collected weekly from the beginning of March until the end of September. Adults were caught from mid-April until the end of May. Every day, during a period of ca. 30 min. around noon, about twenty female wasps and a similar sample of gall midges were collected and subsequently identified.

Host-parasitoid specificity was determined by rearing adult parasitoids from gall samples sorted according to the gall maker. Mortality caused by parasitoids was defined by dissecting gall samples that had been collected in December. All seasonal activities have then ended, but many fruit catkins are still complete and can be collected from the trees.

An extensive description of the study-areas Meijendel (52.08N 4.20E), Duivenvoorde (52.06N 4.24E), Kootwijk (52.11N 5.46E), Ilperveld (52.29N 4.58E) and Nieuwkoop (52.10N 4.50E) was given in Roskam (1977); Hulshorst (52.22N 5.44E) and Kootwijk are dry areas on sand.

ADULTS

Adults of species belonging to *Platygaster* were described by Kieffer (1926) and those of *Metaclisis phragmitis* by Debauche (1947). Therefore, attention will be paid here only to some differential characters.

Metaclisis. — (figs. 1, 5—7, 10, 16). Fore wing with subcostal and medial vein, basal vein indicated by a more or less distinct dark streak, subcostal vein terminated by a distinct stigma, which does not reach the front margin of the wing. Second (sex) flagellomere in male as wide as third, without large, oval sensilla. Proximal part of female second gastral tergite broad, about ⅔ as wide as distal part. Sheaths of ovipositor exposed.

Platygaster. — (figs. 2—4, 8, 9, 11—15). Wing venation reduced. Second (sex) flagellomere of male wider than third, with large, oval sensilla. Proximal part of female gastral tergite about half the width of the distal part.

P. betularia. — Males. Flagellomeres subquadrate, length of fifth flagellomere less than 1.4 times its width in lateral view (fig. 3). Proximal part of scutellum rather dull, due to relatively rich setation (fig. 37).

Females. Scutellum as in male (fig. 39). Gaster twice as long as wide, gradually narrowing towards its apex (fig. 14); exposed part of fifth and sixth segments about a fifth (0.19—0.22, n=5) the length of the gaster without ovipositor; surface of fifth segment shiny, without any sculpture.

P. betulae. — Males. Flagellomeres oblong, length of fifth flagellomere more than 1.4 times its width in lateral view (fig. 4). Proximal part of scutellum shiny, due to relatively sparse setation (fig. 38).

Females. Scutellum as in male (fig. 40). Gaster

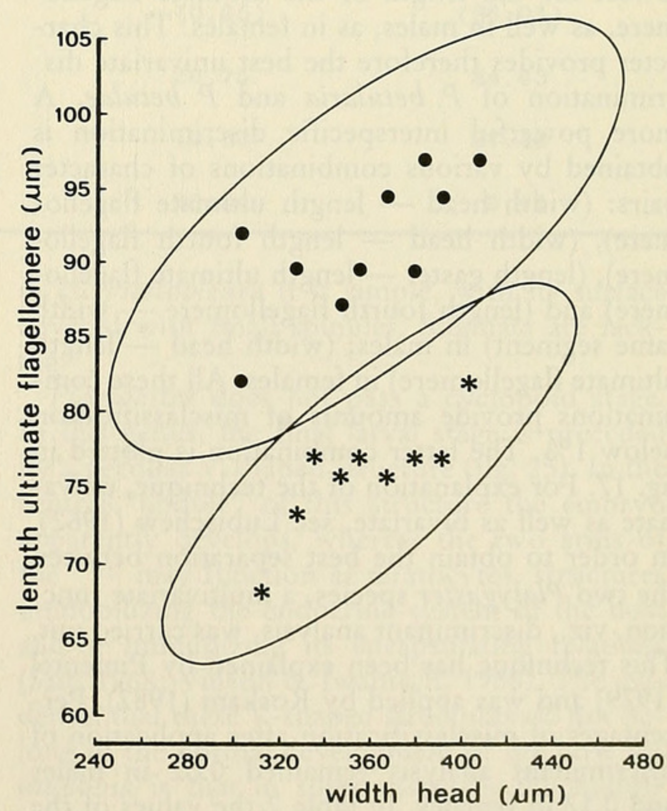


Fig. 17. Species differences in *Platygaster* females. The ellipses indicate 95% confidence limits. Dots, *P. betulae*; asterisks, *P. betularia*.

Table 1. Mean values (x̄) and standard deviations (s) of adult characters, measurements in µm.

	MALES							FEMALES						
	P. betularia ex *S. skuhravae*		*P. betularia* ex *S. betulae*		*P. betulae* ex *S. tarda*		% overlap *b-lae/b-ria*	*P. betularia* ex *S. skuhravae*		*P. betularia* ex *S. betulae*		*P. betulae* ex *S. tarda*		% overlap *b-lae/b-ria*
CHARACTER	x̄	s	x̄	s	x̄	s		x̄	s	x̄	s	x̄	s	
width head	366.6	31.9	369.0	22.2	377.5	25.0	42.9	336.1	23.4	358.7	28.4	357.4	35.5	49.2
length gaster	557.2	55.9	550.8	35.4	544.4	19.5	47.4	590.9	49.1	633.1	60.1	736.0	89.2	24.9
length ult. flagellomere	92.0	6.1	90.8	4.1	106.6	6.1	6.7	75.9	2.9	76.4	3.8	92.0	4.6	3.3
length 4th flagellomere	47.8	5.4	44.7	4.3	58.8	5.5	7.7	45.4	3.5	46.1	5.1	52.7	6.6	28.8
width 4th flagellomere	36.6	3.2	35.6	4.2	37.4	7.4	35.7	28.3	1.7	27.8	2.4	29.0	3.1	41.3

more than twice as long as wide (5:2), distinctly narrowed between fourth and fifth segment (fig. 15); exposed part of fifth and sixth segments about 0.3 times (0.26—0.31, n=5) the length of the gaster without ovipositor; surface of fifth gastral segment with band of longitudinal striae.

Means and standard deviations of five variates for different species of *Platygaster*, as well as for different host groups of *P. betularia*, are presented in table 1. Interspecific percentages of overlap, or percentages of misclassification, are lowest for the length of the ultimate flagellomere, as well in males, as in females. This character provides therefore the best univariate discrimination of *P. betularia* and *P. betulae*. A more powerful interspecific discrimination is obtained by various combinations of character pairs: (width head — length ultimate flagellomere), (width head — length fourth flagellomere), (length gaster — length ultimate flagellomere) and (length fourth flagellomere — width same segment) in males; (width head — length ultimate flagellomere) in females. All these combinations provide amounts of misclassification below 1%. The latter combination is plotted in fig. 17. For explanation of the technique, univariate as well as bivariate, see Lubischew (1962). In order to obtain the best separation between the two *Platygaster* species, a multivariate function, viz., discriminant analysis, was carried out. This technique has been explained by Pimentel (1979) and was applied by Roskam (1982). Percentages of misclassification after application of discriminant analysis remained 0.02 in males and 0.17 in females. In table 2 the values of the character set are summarized. In males, the length of the fourth flagellomere contributes most to discrimination, whereas in females, as was expected on results of univariate analysis, the length of the ultimate flagellomere is most important for species discrimination: these characters scored the highest values as coefficients for the canonical variates, 0.5198 and 0.2914, respectively. The canonical score Z (sum of the products of character values and corresponding coefficients for canonical variates, table 2) is plotted in fig. 41. Identification of new specimens is possible by calculating their canonical score Z (Bigelow & Reimer, 1954; Roskam, 1982). Such identification runs then as follows:

Z males = (length fourth flagellomere) + 0.32 (length ultimate flagellomere) −0.21 (width head) < 4 .... *P. betularia*

Z males = Idem > 4 .... *P. betulae*

Z females = (length ultimate flagellomere) + 0.47 (length fifth flagellomere) − 0.68 (width fourth flagellomere) < 84 .... *P. betularia*

Z females = Idem > 84 .... *P. betulae*

P. betularia has been reared in considerable numbers from two different hosts, *Semudobia skuhravae* and *S. betulae*. No discrimination between specimens reared from different hosts was possible in an univariate way (table 1). Also in a multivariate way, viz., discriminant analysis, no discrimination was possible between subgroups of *P. betularia* which developed in different host species: in males misclassification remained 40.5%; in females 32.3%. Hence, the influence of the host on the adult morphology of *P. betularia*, if present, is very small and remains below the resolving power of even this sophisticated technique.

Table 2. Summary of discriminant analyses. Values in brackets not used for calculation of canonical score Z. For further explanation, see text.

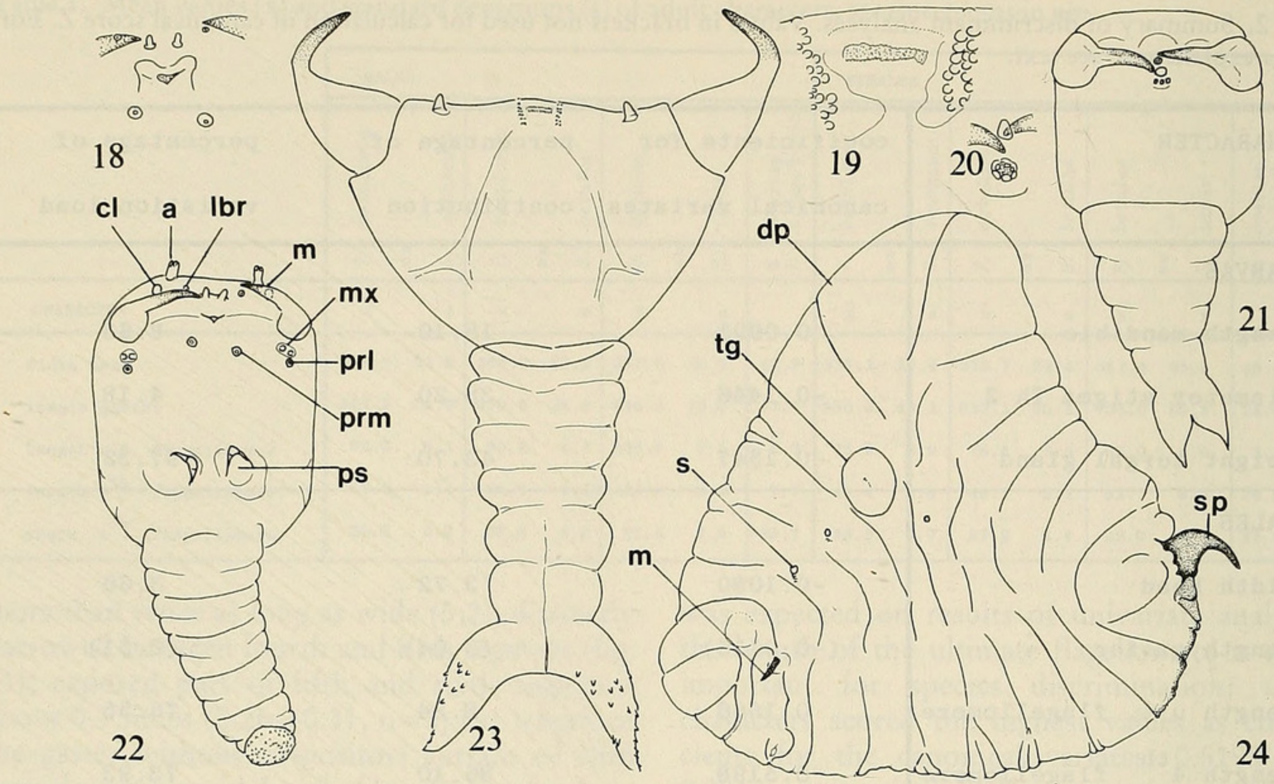
CHARACTER	coefficients for canonical variates	percentage of contribution	percentage of variation load
LARVAE			
length mandible	0.0995	18.10	8.63
diameter stigma Th 2	-0.1446	38.20	4.18
height tergal gland	-0.1547	43.70	97.32
MALES			
width head	-0.1080	3.72	3.60
length gaster	(-0.0116)	(0.04)	(0.51)
length ult. flagellomere	0.1666	8.84	75.55
length 4^{th} flagellomere	0.5198	86.10	73.93
width 4^{th} flagellomere	(-0.0638)	(1.30)	(14.03)
FEMALES			
width head	(-0.0833)	(4.53)	(0.04)
length gaster	(-0.0192)	(0.25)	(36.01)
length ult. flagellomere	0.2914	56.75	84.43
length 4^{th} flagellomere	0.1358	12.33	27.46
width 4^{th} flagellomere	-0.1974	26.04	5.44

IMMATURE STAGES

The larval phase of many Platygastridae is characterized by hypermetamorphosis: there are two distinct larval stages, which are very different in shape (Leiby & Hill, 1924).

First instar larvae of forms in which hypermetamorphosis occurs have a cyclopoid shape (figs. 21—23). They consist of a cephalothorax with huge mandibles to which a slender, 5—7 segmented abdomen is attached. Antennae are simple, conical. The surrounding of the mouth is sclerotized and differently shaped in the various forms (figs. 18—20). Maxillary sensillae are only distinct in the form attributed to *Piestopleura* (fig. 22). In this form the cephalothorax bears two pseudopodia. In *Metaclisis* the abdominal segments are simple, whereas in cf. *Piestopleura* they seem to be secondarily subdivided. The final segment of *Metaclisis* is bilobed, in cf. *Piestopleura* it is simple, with its surface covered with small spinules. Stigmata are lacking.

Platygaster does not pass a cyclopoid stage. In this genus, the final larval stage is preceded by a peculiar V-shaped structure (fig. 25). In the central "nodule" of this structure the embryo apparently develops, whereas the two arms of the "V" may function as teratocytes, structures immobilizing the endocrine system of the host and/or immunizing its encapsulating relations (Salt, 1968; Vinson & Iwantsch, 1980). The evidence, that these V-shaped structures do not belong to the normal development of the host *Semudobia* is that in some instances the nodule becomes encapsulated by melanin. Although some extensive reports on early developmental stages of *Platygaster* exist (Marchal, 1906; Silvestri, 1916; Leiby & Hill, 1924; Hill & Emery,



Figs. 18—24. Larval platygastrid characters. 18—20, detail of oral region; 21—23, cyclopoid larval stage, ventral aspect; 24, full grown larval stage, lateral aspect. 18—22, endoparasitoids of *Dasineura interbracta*; 23, *Metaclisis phragmitis*; 24, endoparasitoid of *Semudobia brevipalpis*. a, antenna; cl, clypeal sensilla; dp, dorsal protuberance; lbr, labral sensilla; m, mandible; mx, maxillary sensilla; prl, lateral prelabial sensilla; prm, median prelabial sensilla; ps, pseudopodium; s, stigma; sp, spine-like outgrowth; tg, tergal gland. 23, 24 × 100; 21, 22, × 240; 18—20, × 400.

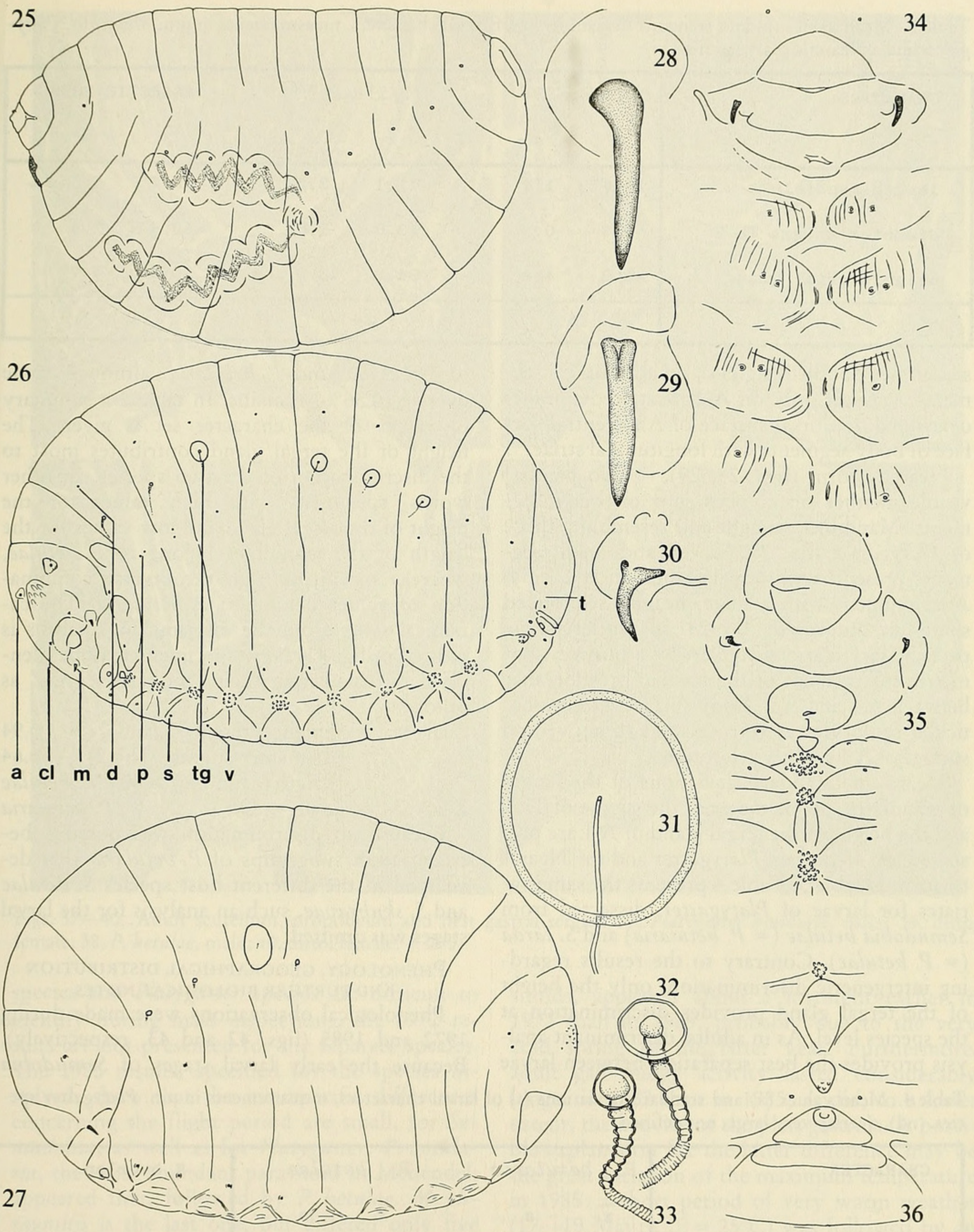
1937; Clausen, 1956), V-shaped structures, in connexion to platygastrid parasitation, remained unobserved.

After a moulting, final instar larvae develop from these primary stages. The terminology of the structures has been treated by Roskam (1982). The final larval stage is apodous and consists of a head, three thoracic segments (Th 1—3) and seven or eight abdominal segments (A 1—8) of which the final one is the anal segment (AS). The antennae are simple and inconspicuous. The clypeus bears one pair of papillae on which a seta may be developed. Mandibles are distinct. No sensillae are visible on the underlip complex.

Second and third thoracic segments, and the second abdominal segment bear a pair of functional stigmata (figs. 26—27); the first abdominal segment, and in *Metaclisis* also the abdominal segments A 3—5, bear an oval, shallow, plate-like structure, in the centre of which a vestigial stigma is present (fig. 31). Silvestri (1916) made histological cross sections of these structures and named them tergal glands. He supposed these glands to have a function during pupation of the parasitoid. Rows of papillae are present on dorsal, pleural and ventral surfaces of the body segments. Final instar larvae of *Metaclisis*, the two *Platygaster* species and the Nearctic form differ as follows.

Metaclisis phragmitis (figs. 26, 30, 33, 35—36). — Clypeal papillae with short seta. Mandibles small and curved (fig. 30). Eight abdominal segments present, with tergal glands on A 1, A 3—5. Papillary pattern rather complete, with one pair of rows of dorsal papillae, one pair of rows of pleural papillae and one pair of rows of sternal papillae (on thoracic segments) and ventral papillae (on abdominal segments). Two pairs of terminal papillae on dorsal surface of the anal segment. Dorsal papillae lacking on A 6 and A 7, pleural papillae sometimes doubled on Th 2 and Th 3. Ventral body surface with rounded verrucae.

Platygaster (figs. 27, 28, 31, 32, 34). — Clypeal papillae without seta. Mandibles straight and about twice as large as those of *Metaclisis* (fig. 28). Seven abdominal segments present, with tergal glands on A 1 only. Papillary pattern reduced and variable. Dorsal papillae usually absent. Pleural papillae only on Th 2 and Th 3 and, two pairs, on A 7. Sternal papillae,



Figs. 25—36. Larval platygastrid characters. 25, third instar host larva with V-shaped endoparasitoid stage, lateral aspect; 26, 27, full grown endoparasitoid larva, latero-ventral aspect; 28—30, mandible of full grown endoparasitoid larva; 31, tergal gland on first abdominal segment of full grown larva; 32, 33, stigma on second thoracic segment of full grown larva; 34, 35, head and sternal aspect of full grown larva; 36, ultimate and penultimate segments of full grown larva, ventral aspect. 26, 30, 33, 35, 36, *Metaclisis phragmitis*; 25, 27, 28, 31, 32, 34, *Platygaster betularia;* 29, platygastrid endoparasitoid of *Semudobia brevipalpis*. a, antenna; cl, clypeal sensilla; d, dorsal papilla; m, mandible; p, pleural papilla; s, sternal papilla; t, terminal papilla; tg, tergal gland; v, ventral papilla. 25, × 50; 26, 27, × 60; 34—36, × 150; 28—33, × 720.

Table 3. Mean values (x̄) and standard deviations (s) of larval characters, measurements in µm. *Metaclisis, Platygaster* and a Nearctic platygastrid.

CHARACTER	*METACLISIS*		*PLATYGASTER*		NEARCTIC FORM	
	x̄	s	x̄	s	x̄	s
length mandible	19.5	1.4	41.1	3.5	35.7	3.5
diameter stigma Th 2	8.7	0.8	13.0	1.6	10.4	1.4
height tergal gland	43.9	4.8	94.2	13.0	70.2	4.7
n	15		24		9	

sometimes doubled (fig. 34), on all thoracic segments, ventrals only on A 1. Scattered spinules developed on dorsal surface of AS. Ventral surface of body segments with longitudinal striae.

Nearctic form (figs. 24, 29). — No papillae visible, neither on clypeus, nor on body segments. Mandibles straight and resembling those of *Platygaster* (fig. 29). Seven abdominal segments present, with tergal glands on A 1 only. Anal segment with a huge, heavily sclerotized spine-like outgrowth (fig. 24: sp). In lateral aspect the larvae are triangular, by a bizarre, allometric enlargement of the median protuberance between A 1 and A 2. Body surface without cuticular sculptures as verrucae and striae; ventral surface of A 5 slightly sclerotized.

Means and standard deviations of the length of mandibles, the diameter of the stigma of Th 2 and the height of the tergal gland of A 1 are presented for *Metaclisis, Platygaster* and the Nearctic form in table 3. Table 4 presents the same variates for larvae of *Platygaster*, dissected from *Semudobia betulae* (= *P. betularia*) and *S. tarda* (= *P. betulae*). Contrary to the results regarding intergeneric discrimination, only the height of the tergal gland provides discrimination at the species level. As in adults, discriminant analysis provides the best separation between larvae of *P. betulae* and *P. betularia*, although some overlap (6.36%) remains. In table 2 a summary of values of the character set is given. The height of the tergal gland contributes most to the discrimination of the two species. In other words, specimens with high values for the height of the tergal gland and low values for the length of the mandibles belong to *P. betulae*, whereas specimens with the inverse combination of values belong to *P. betularia*. The canonical score from the discriminant analysis is plotted in fig. 41. New specimens may be identified by calculating their canoncial score Z as follows:

Z larvae = (height tergal gland) + 0.94 (diameter stigma Th 2) − 0.64 (length mandible) > 80 *P. betulae*
Z larvae = Idem < 80 .... *P. betularia*

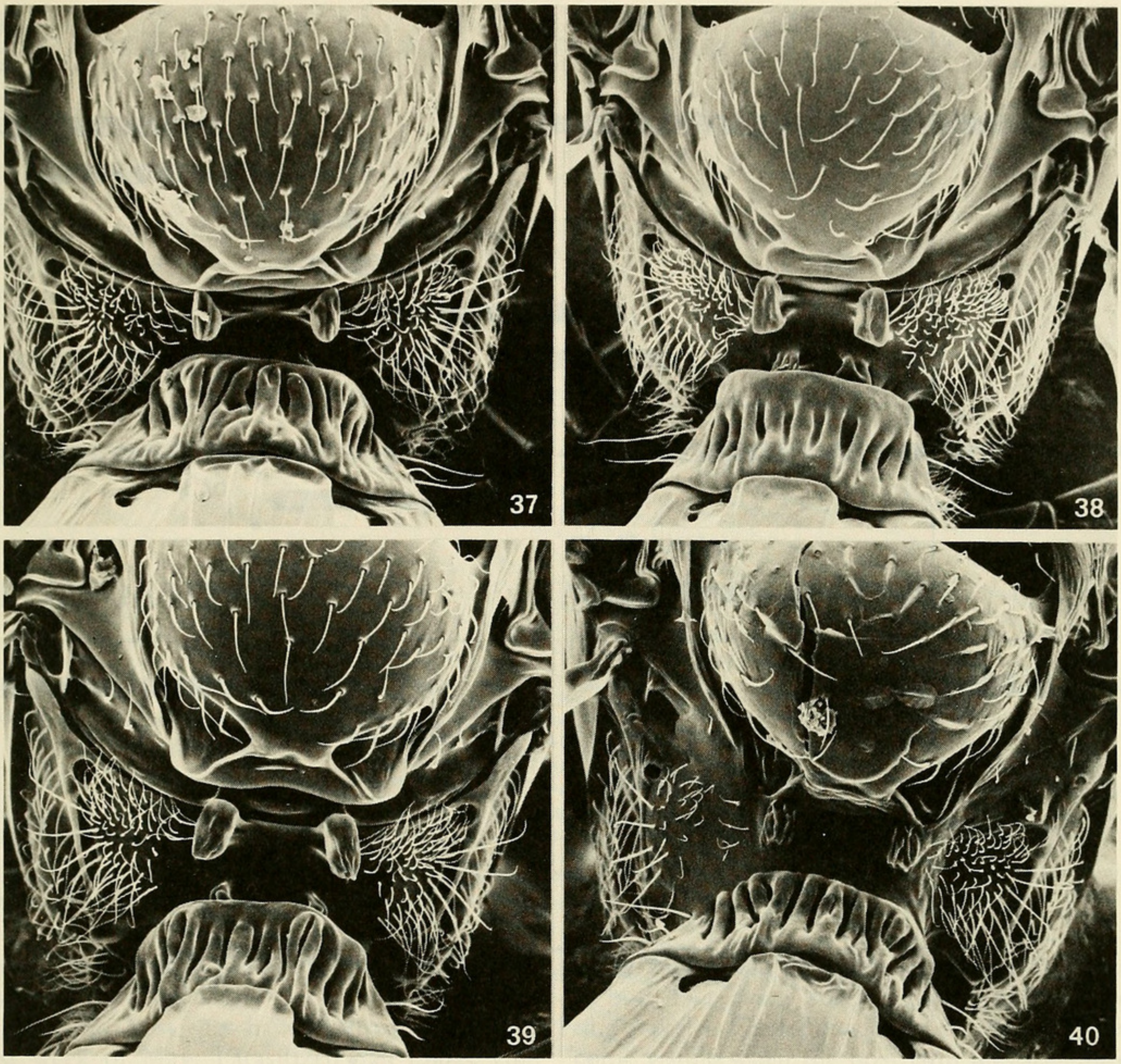
Because no discrimination was possible between adult subgroups of *P. betularia* that developed in the different host species *S. betulae* and *S. skuhravae*, such an analysis for the larval stages was omitted.

PHENOLOGY, GEOGRAPHICAL DISTRIBUTION AND FURTHER BIOLOGICAL NOTES

Phenological observations were made during 1972 and 1985 (figs. 42 and 43, respectively). Because the early larval stages of *Semudobia*

Table 4. Mean values (x̄) and standard deviations (s) of larval characters, measurements in µm. *Platygaster* species. (nd), overlap very large, not defined.

CHARACTER	*P. betularia*		*P. betulae*		% overlap
	x̄	s	x̄	s	
length mandible	40.4	4.8	42.3	2.4	40.3
diameter stigma Th 2	12.8	1.0	13.4	2.1	(nd)
height tergal gland	81.6	8.3	105.6	5.7	4.8
n	9		10		



Figs. 37—40. Adult scutellum, propodeum and first gastral tergite. 37, *Platygaster betularia*, male; 39, ditto, female; 38, *P. betulae*, male; 40, ditto, female. × 250.

species and *Platygaster* species are difficult to identify during mass inspections, the 1972 results are not presented for the separate species. The 1985 results, specified for the species involved, show that the interspecific differences concerning the flight period are small, for *Semudobia*, as well as for *Platygaster*. *P. betularia*, the most abundant parasitoid in Meijendel, appeared first, followed by *P. betulae*. *M. phragmitis* is the last one, but differed only five days with *P. betularia*. All parasitoid species have a considerably longer flight period than their hosts. The slight difference between *P. betularia* and *P. betulae* is corresponding to the difference of maximum activity of their respective hosts, *S. betulae* and *S. tarda*.

Adult stages of gall midges, as well as of parasitoids, appeared about a fortnight earlier in 1972 than in 1985, probably due to the very cold spring of the latter year. Furthermore, adult gall midge activity lasted considerably longer in 1972 than in 1985, as did, to a lesser extent, the activity of the platygastrids. A possible explanation for the latter difference may be the great variation of the maximum temperature in 1985: a short period of very warm weather (17—19 May; t_{max} = 25°C) was followed by an extraordinarily cold period (23—24 May; t_{max} = 12°C).

Platygaster — In the field, adult emergence coincides with the appearance of *Semudobia* females. Ovipositing gall midges and parasitoids frequently occur together on the same flowering birch catkin, but in other instances *Platygaster*

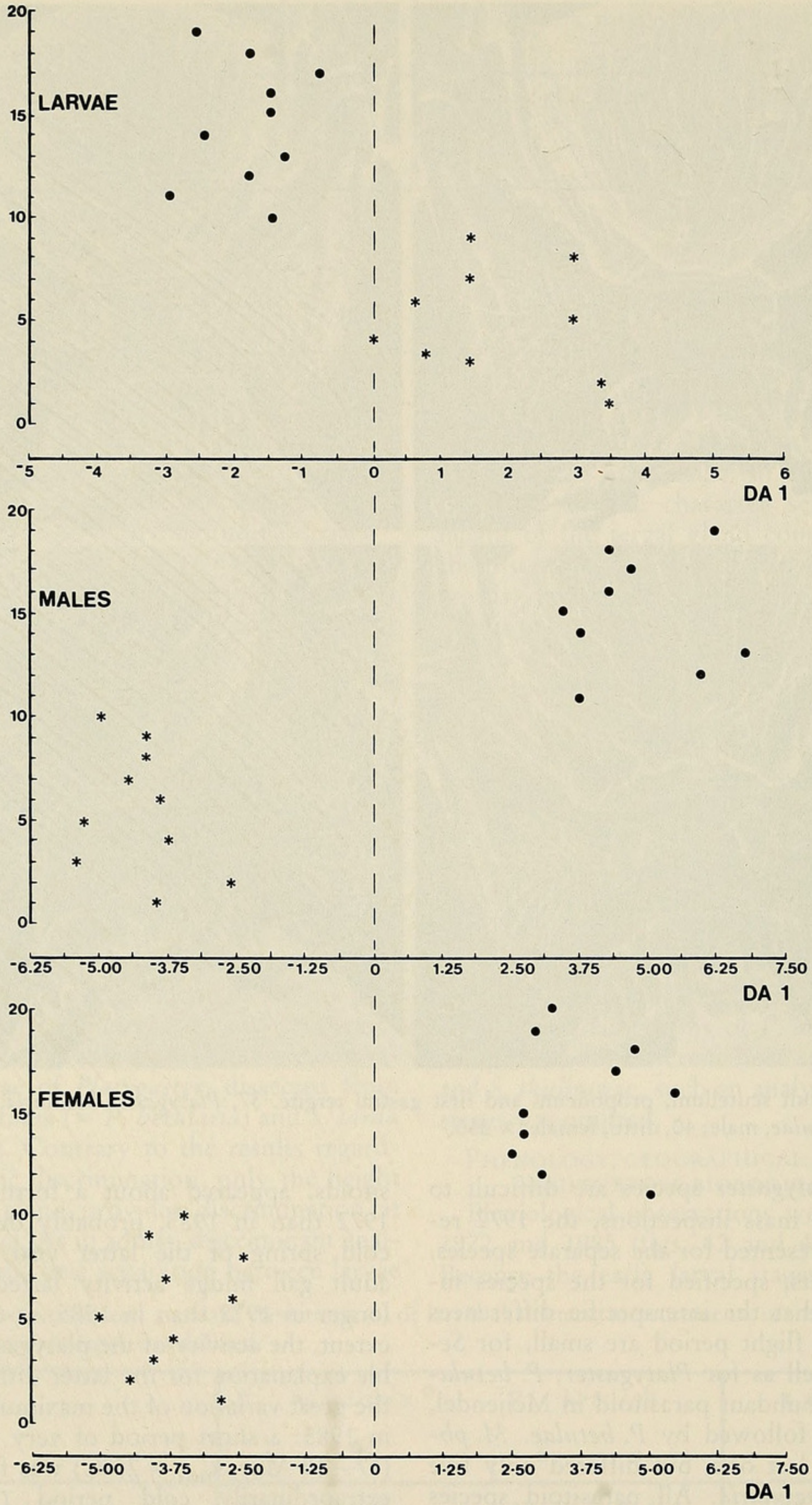


Fig. 41. Two group discriminant space. Y-axis represents only the sequence of specimens. DA 1, first discriminant axis; dots, *Platygaster betulae*; asterisks, *P. betularia*.

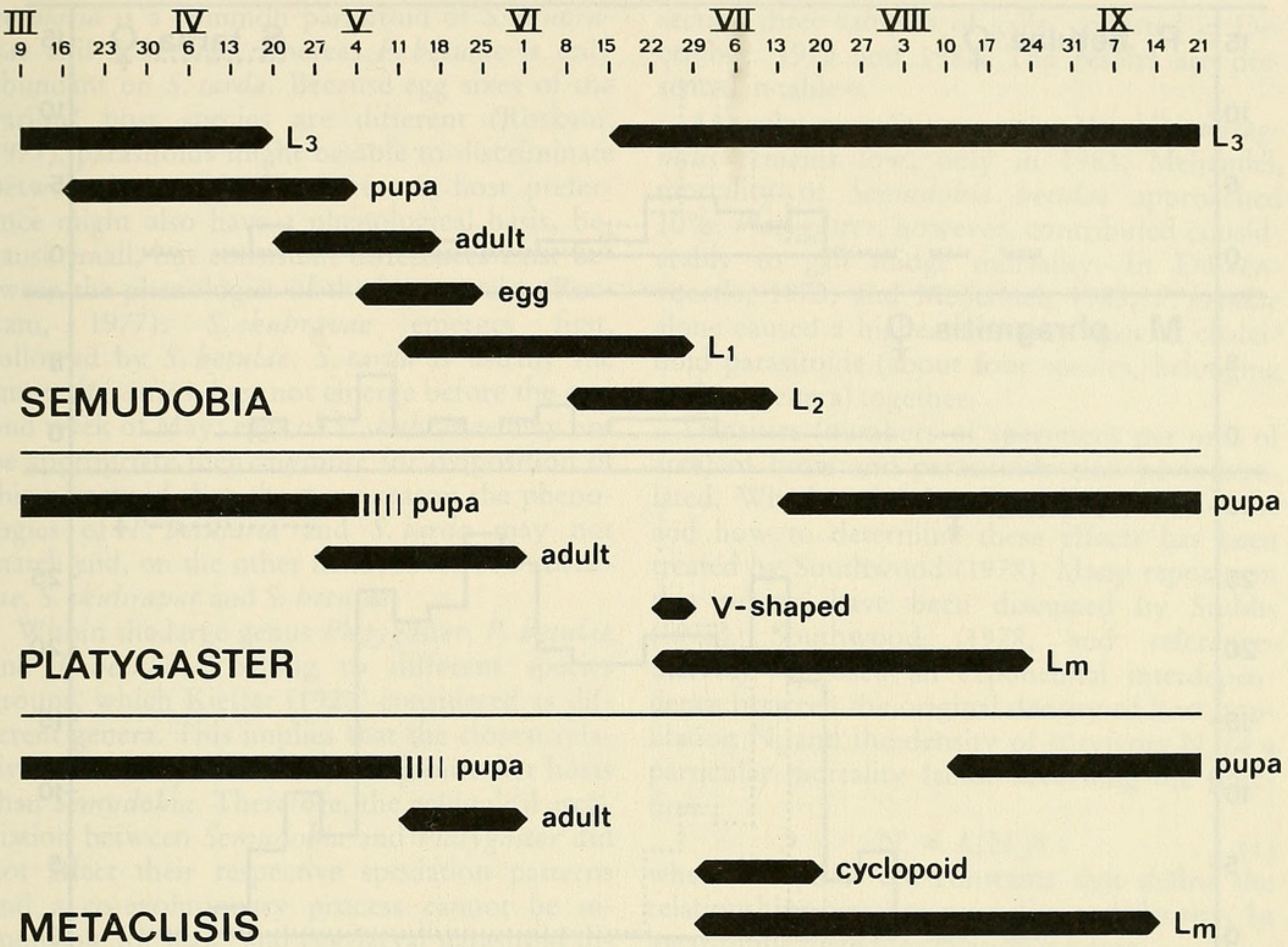


Fig. 42. Phenology of platygastrid parasitoids, Meijendel, 1972. L1, L2, L3, Lm: first, second, third, full grown larval instar, respectively.

females search for host eggs in absence of *Semudobia*. Adult parasitoid activity ceases when most of the host eggs have been eclosed in the last week of May. Parasitized gall midge embryo's apparently develop in a normal way. Hatched host larvae with dormant parasitoids mine into ovaries of *Betula* and induce galls as do healthy larvae. Not before the host reaches its early third instar, signs of parasitation appear. The host becomes less mobile and looses its bright orange colour. In this stage the V-shape "teratocyte stage" becomes apparent. From the end of June until mid-August the final instar larva fills about the whole body content of its host. From the end of July parasitoids pupate, remaining within the host skin and filling about half the room with meconium. In the second half of August the pupa is dark, fully sclerotized and looses its exuviae. The adult overwinters in a quiescent condition and leaves the gall when the temperture rises at the end of April of the following year.

Metaclisis. — This parasitoid is about a week later in development than *Platygaster*. The period of adult flight is somewhat shorter than that of both *Platygaster* species; it lasts only two to three weeks. Cyclopoid larvae of *Metaclisis* become visible when the host is in its early third (final) instar, as does the V-shaped stage of *Platygaster*. The cyclopoid stage, however, lasts considerably longer than the V-shaped one.

Platygaster and *Metaclisis* were present in all samples collected in North-Western Europe, Switzerland and Poland. *Platygaster* was also reared from samples collected in Wladiwostok, U.S.S.R. and Sapporo, Japan. The lack of *Metaclisis* in these samples may be attributed to small sample sizes. Parasitoids belonging to *Platygaster* and *Metaclisis* are absent from the Nearctic: over 70 samples collected in Canada (Alberta and Quebec) and U.S.A. (Pennsylvania, Ohio, Illinois, South Dakota, Montana, Wyoming and Colorado) contained abundant *Semudobia* galls, but were free from these parasitoids. The undescribed platygastrid endoparasitoid was dissected from galls induced by *S. brevipalpis* Roskam in fruit catkins of *Betula populifolia* Marsh. (Pennsylvania, Catskill formation, Long Pond,

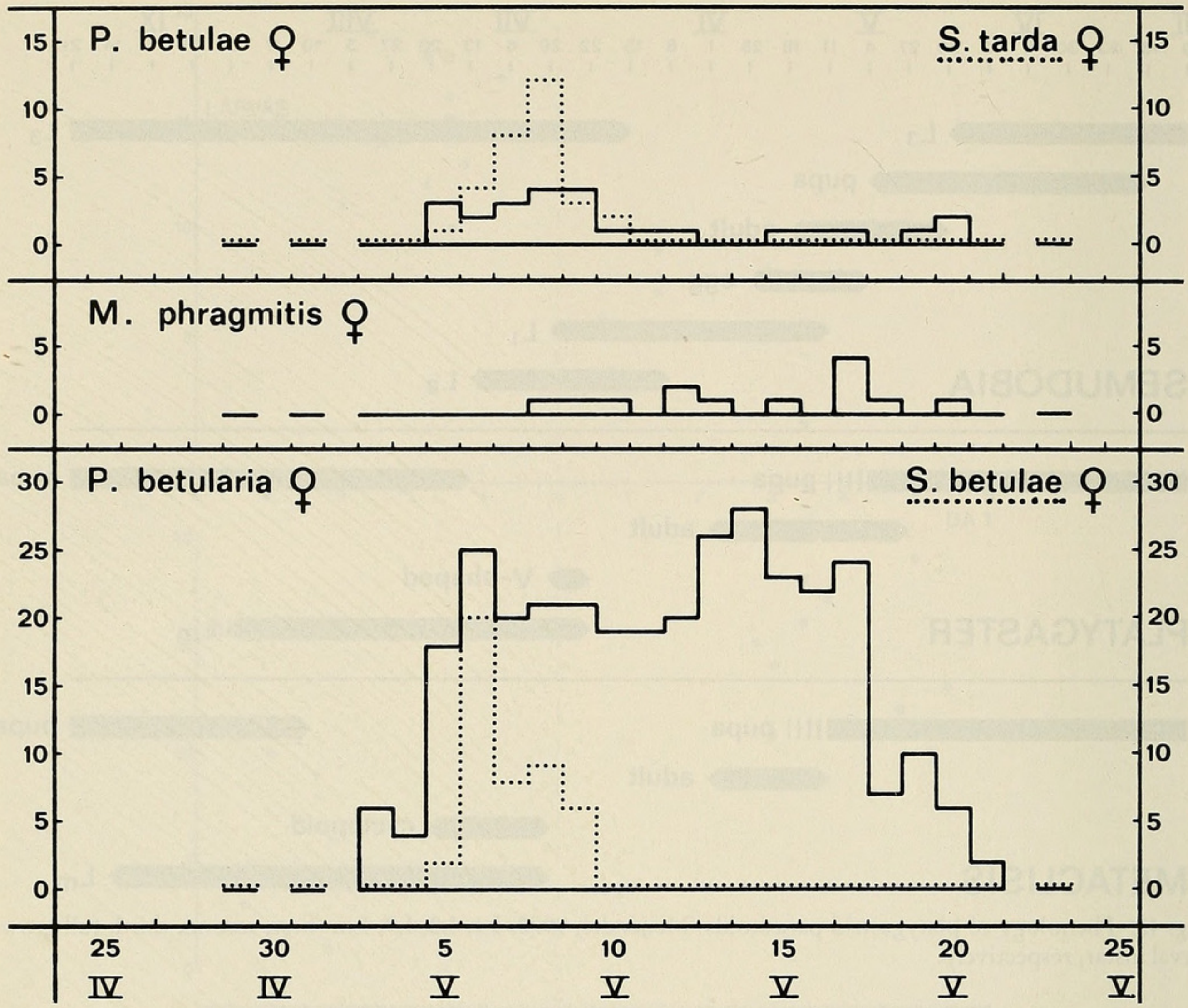


Fig. 43. Field captures of adult platygastrid parasitoids, Meijendel, 1985. Drawn lines, parasitoid females; dotted lines, host females.

Luzerne County, Leg. A. A. Heller & E. Gertrude Halbach, 16—17.ix.1892). Not only egg-larval parasitoids, one sample with the undescribed form excepted, but also inquiline gall midges are absent from Nearctic samples (Roskam, 1979). Hence, Nearctic insect communities centered upon *Semudobia* are less diverse than Palaearctic ones: two complete segments of the food web, including important mortality factors in the Palaearctic, are missing in the Nearctic.

Endoparasitoids of *Dasineura*. — Two gall midge species, viz., *D. fastidiosa* Roskam and *D. interbracta* Roskam occur frequently in birch catkins. They are inquilines (food parasitoids) of *Semudobia* species (Roskam, 1979). Cyclopoid stages of platygastrid endoparasitoids (figs. 21, 22) were dissected from *Dasineura* larvae collected from 7.vi.—3.vii.1978, Meijendel, and on 20.vii.1977, Norway, Åseral. Because *Dasineura* larva drop onto the ground before the parasitoids reach the full grown instar, this stage has not been observed and adults could not be reared.

In each parasitized *Dasineura* larva usually two parasitoids, attributed to *Piestopleura*, are present. The pairs of parasitoids are supposed to be twins as the result of polyembryonic development. A twinning development was earlier reported for another platygastrid, namely, *Platygaster hiemalis* Förster (Leiby & Hill, 1923).

PARASITOID SPECIFICITY

In order to determine host — parasitoid specificity, adult parasitoids have been reared from sorted samples. The results are presented in table 5.

Metaclisis phragmitis, although less common than both *Platygaster* species, is a regular parasitoid of *S. betulae* and *S. tarda*, but could only be reared once from *S. skuhravae*. *Platygaster* *betularia* is a common parasitoid of *S. skuhravae* and *S. betulae*, whereas *P. betulae* is only abundant on *S. tarda*. Because egg sizes of the various host species are different (Roskam, 1977), parasitoids might be able to discriminate between host eggs. Furthermore, host preference might also have a phenological basis, because small, but consistent differences exist between the phenologies of the host species (Roskam, 1977): *S. skuhravae* emerges first, followed by *S. betulae; S. tarda* is usually the latest. *Metaclisis* does not emerge before the second week of May; eggs of *S. skuhravae* may not be appropriate then anymore for oviposition of this parasitoid. For the same reason the phenologies of *P. betularia* and *S. tarda* may not match and, on the other hand, those of *P. betulae, S. skuhravae* and *S. betulae.*

Within the large genus *Platygaster, P. betulae* and *P. betularia* belong to different species groups, which Kieffer (1926) considered as different genera. This implies that the closest relatives of both species did develop on other hosts than *Semudobia*. Therefore, the ecological association between *Semudobia* and *Platygaster* did not affect their respective speciation patterns and a co-evolutionary process cannot be responsible for host- and egg-larval parasitoid diversity. This is probably in contrast with the speciation patterns of the food parasitoids, viz., *Dasineura interbracta* and *D. fastidiosa* (Roskam, 1979), and some of the chalcidoid parasitoids (Roskam, in preparation).

HOST MORTALITY

Host mortality has been determined by dissecting three samples of galls, collected in December, 1975 and 1983. The results are presented in table 6.

As a rule, mortality caused by *Metaclisis phragmitis* remains low; only in 1983, Meijendel, mortality of *Semudobia betulae* approached 10%. *Platygaster*, however, contributed considerably to gall midge mortality. In Duivenvoorde, 1975, and Meijendel, 1983, *P. betulae* alone caused a higher mortality than all chalcidoid parasitoids (about four species, belonging to three genera) together.

Densities (numbers of specimens per unit of area) of hosts and parasitoids may be interrelated. Whether density-dependent effects exist and how to determine these effects has been treated by Southwood (1978). Many reports on this subject have been discussed by Stubbs (1977). Southwood (1978, and references therein) supposed an exponential interdependence between the original density of host population N_t and the density of survivors N_s of a particular mortality factor according the function.

$$N_s = A(N_t)^B \qquad (1)$$

where A and B are constants that define the relationships between mortality and density. In logarithmic form the equation is linear

$$\text{Log } N_s = \log A + B \log N_t \qquad (2)$$

where B defines the slope of the regression line of log N_s over N_t. When B does not depart significantly from 1, a density-dependent effect is absent. However, when $B < 1$, the mortality factor has a positive density-dependent effect: high host densities (aggregated situations) suffer proportionally more than low densities. $B > 1$

Table 5. Parasitoid specificity regarding various *Semudobia* hosts.

		SEMUDOBIA SKUHRAVAE									SEMUDOBIA BETULAE									SEMUDOBIA TARDA								
			M. phragmitis		*P. betulae*		*P. betularia*					*M. phragmitis*		*P. betulae*		*P. betularia*					*M. phragmitis*		*P. betulae*		*P. betularia*			
AREA	YEAR	HOST	♂	♀	♂	♀	♂	♀	CHALCIDOID PARASITOIDS	TOTAL	HOST	♂	♀	♂	♀	♂	♀	CHALCIDOID PARASITOIDS	TOTAL	HOST	♂	♀	♂	♀	♂	♀	CHALCIDOID PARASITOIDS	TOTAL
Hulshorst	1979	-	-	-	-	-	-	-	4	4	7	-	-	-	-	15	31	153	206	1	-	-	-	1	-	-	44	46
Kootwijk	1979	2	-	-	-	-	-	2	7	11	8	-	2	-	-	1	9	69	89	-	-	-	-	-	-	-	2	2
Meijendel	1977	146	-	1	-	-	12	7	134	300	156	13	17	-	-	21	57	213	477	101	44	32	71	80	-	3	148	479
Meijendel	1979	13	-	-	1	1	22	59	19	115	43	1	3	-	-	15	46	303	411	93	3	8	17	60	1	5	140	327
Duivenvoorde	1979	2	-	-	-	-	2	7	22	33	21	5	7	-	-	4	5	76	118	2	-	2	7	16	-	1	122	145
Ilperveld	1979	4	-	-	-	-	-	-	4	8	21	4	3	-	-	8	29	73	138	14	1	3	-	13	-	-	164	195
Nieuwkoop	1979	-	-	-	-	-	-	4	107	111	38	11	11	-	-	26	116	186	388	6	1	2	2	13	-	-	110	134
TOTAL		167	-	1	1	1	36	79	297	582	294	34	43	-	-	90	293	1073	1827	217	49	47	92	183	1	9	730	1328

Table 6. Mortality (%) caused by parasitoids. —, not defined.

HOST	AREA	YEAR	NR. of GALLS	*PLATYGASTER*	*METACLISIS*	CHALCIDOIDS	INQUILINES
S. skuhravae							
	Duivenvoorde	1975	16	6.3	0	6.3	-
	Meijendel	1975	1	0	0	0	-
	Meijendel	1983	78	14.1	0	19.1	0
S. betulae							
	Duivenvoorde	1975	133	11.3	2.3	25.6	-
	Meijendel	1975	1019	12.9	0	46.0	-
	Meijendel	1983	231	9.1	9.5	26.8	10.4
S. tarda							
	Duivenvoorde	1975	534	24.3	2.6	7.3	-
	Meijendel	1975	399	6.3	1.5	28.1	-
	Meijendel	1983	894	22.7	3.8	19.2	18.5

represents the inverse situation: density dependence is negative, low host densities (segregated situations) become proportionally more severely attacked. The intercept of the regression line, log A, is not further considered; the meaning of this constant is discussed by Hassell (1975).

In order to determine the density-dependent effect of *Platygaster*, two samples of catkins (ten per tree) were collected in Meijendel, December 1982 and 1983. Because each catkin was considered a functional unit of area, a patch, the numbers of galls (N_t) and of galls without *Platygaster* parasitation (N_s) were defined per catkin. Interference between *Platygaster* and other parasitoids was not considered because chalcidoid

Table 7. Density-dependent host mortality. (★), significant, $p < 0.05$.

HOST	YEAR	MEAN NR. of GALLS per CATKIN	NR. of CATKINS with GALLS	NR. of CATKINS with *PLATYGASTER*	NR. of GALLS in EMPTY PATCHES	NR. of GALLS in LOCALIZED PATCHES	B- VALUE
S. skuhravae	1982	0.16	25	4	45	7	-
	1983	1.52	17	7	33	45	-
S. betulae	1982	1.01	77	25	184	148	1.13*
	1983	4.62	37	12	117	114	0.97
S. tarda	1982	1.52	69	40	145	357	1.05
	1983	17.88	43	29	48	846	1.12*

parasitoids either refuse host larvae with *Platygaster* parasitoids (adults), or perish on such hosts (larvae). Galls attacked by inquiline *Dasineura*, which indeed may contain parasitized *Semudobia* larvae, have not been considered too, because it appeared impossible to determine parasitation of such hosts.

Two aspects become distinct from an analysis of the results (table 7). First, gall midge densities vary considerably among different years. *S. skuhravae*, as well as *S. tarda*, caused in 1983 a tenfold of the galls of the preceding year and *S. betulae* produced four times more. Large differences among generations of different years have also been found for other gall midge species and may occur commonly (Skuhravá et al., 1984). The mechanisms that cause such large fluctuations are not well understood.

Second, *Platygaster* species indeed have different effects upon different gall midge densities. Only about one third, or less, of catkins with galls in low densities (those of *S. skuhravae* and *S. betulae*, 1982), but about two third of catkins with galls in high densities (*S. tarda*, 1983) contained parasitized gall midge larvae. This means that many low density patches remained unnoticed („not localized") by ovipositing parasitoids and may therefore function as escape possibilities for the midges. In high density situations (*S. tarda*, 1983), almost all galls occur in catkins found by parasitoids. If B-values are defined for patches, visited by parasitoids, a rather surprising result emerges: either B does not significantly depart from 1 (*S. betulae — P. betularia*, 1983; *S. tarda—P. betulae*, 1982), which means that the parasitoids are unable to regulate the host densities; or B is significantly larger than 1 (*S. betulae—P. betularia*, 1982; *S. tarda—P. betulae*, 1983; fig. 44), which means that in those cases the parasitoids have a negatively density-dependent impact on their hosts. Moderate (and, when localized, low) host densities suffer more than high ones. Hence, in localized catkins, escape possibilities for the midges are larger in patches with high densities.

Combining the outcome for localized and not localized catkins, the conclusion is that *Platygaster* parasitoids may be able to eliminate moderate host densities. Escape possibilities for the gall midges remain in both tails of their density distribution: in highly segregate, as well as in highly aggregate situations.

CONCLUSIONS

1. Adult *Platygaster betularia* and *P. betulae* can be distinguished by a combination of antennal characters; larvae by a combination of characters regarding the height of the tergal gland, the diameter of the stigma on the second thoracic segment and the length of the mandibles.

2. No discrimination is possible between subgroups of a parasitoid species that developed in different host species (e.g. *P. betularia* reared from *S. skuhravae* or *S. betulae*).

3. All platygastrid egg-larval parasitoids develop highly synchronized with their hosts. *Metaclisis phragmitis* develops about one week later than both *Platygaster* species. This pheno-

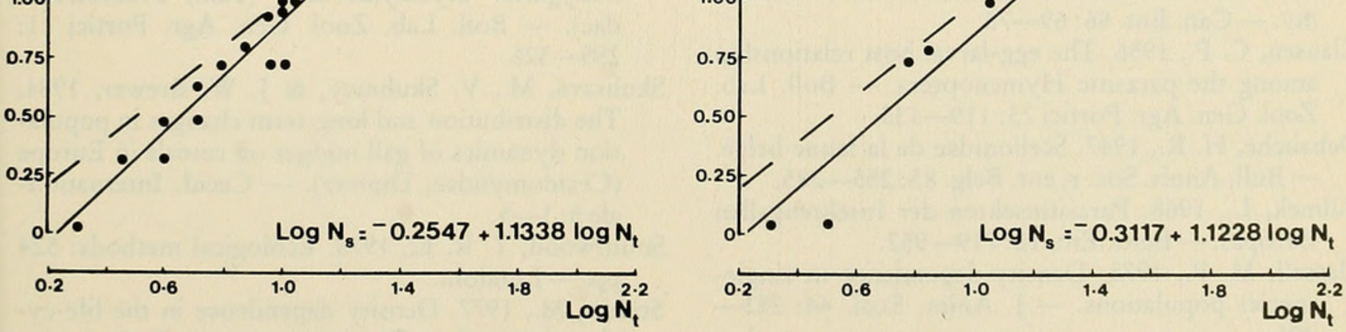


Fig. 44. Density-dependent host mortality. B, slope of the regression line; N_s, density of survivors; N_t, original density of host population. Drawn line, regression of N_s over N_t; dashed line B = 1. Left graph, *Platygaster betularia* on *Semudobia betulae*, Meijendel, 1982; right graph, *P. betulae* on *S. tarda*, Meijendel, 1983. For further explanation, see text.

logical difference might explain the absence of *Metaclisis phragmitis* from *S. skuhravae*.

4. *Platygaster* has been reared from Western and Eastern Palaeartctic localities. *Platygaster* and *Metaclisis* are absent from Nearctic *Semudobia* galls. One Nearctic collection of an unknown egg-larval parasitoid excepted, the whole guild of egg-larval parasitoids is absent from this region, as is the guild of inquilines.

5. Almost complete separation exists in the host preference of the two *Platygaster* species: *P. betularia* is a common parasitoid of *S. skuhravae* and *S. betulae*, whereas *P. betulae* is common on *S. tarda. Metaclisis phragmitis*, one collection excepted, has not been reared from *S. skuhravae*.

6. Diversity of egg-larval parasitoids and their hosts is not a result of co-evolution, because *P. betularia* and *P. betulae* belong to different species groups, whereas *Semudobia* species are close relatives.

7. *Platygaster* species are important mortality factors of *Semudobia* species and may have a density-dependent impact on their hosts. Escape possibilities for *Semudobia* are largest in highly aggregate situations, as well as in highly segregate ones.

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