Systematic Entomology (1994) **19**, 119–132

Morphometric variation in the *Geoica utricularia* (Homoptera: Aphididae) species group on *Pistacia* (Anacardiaceae), with descriptions of new species and a key to emigrant alatae

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Abstract. Variation within and between samples of emigrant alatae from galls on identified *Pistacia* species was studied using bivariate and multivariate techniques. The *Geoica utricularia* complex seems to include at least five taxa, including two newly identified; *G.utricularia* Passerini sensu stricto, on *Pistacia terebinthus*; *G.muticae* Mordvilko, on *P.mutica*; *G.rungsi* Davatchi & Remaudière, on *P.atlantica*; *G.harpazi* sp.n., also on *P.atlantica*; and *G.wertheimae* sp.n. on *P.palaestina*. The emigrant alatae of the two new species are described, together with apterous exules reared from them, and a key is provided to emigrant alatae of all eight *Geoica* species now known to induce galls on *Pistacia*. The taxonomic status of anholocyclic, grass-feeding populations in the *Geoica utricularia* group is discussed.

Introduction

Aphids of the genus *Geoica* (Pemphiginae: Fordini) form leaf galls on *Pistacia* trees (the primary host) in the Mediterranean region and south-west and south Asia. They have a complex 2-year life-cycle that includes migration to and from Gramineae (their secondary host), where all-female (thelytokous) populations feed on the roots. The *Pistacia*-galling and grass-root-feeding forms of the same species are very different morphologically and have been in some cases originally described in different genera.

Populations can persist throughout the year on roots of Gramineae, and such populations occur outside the range of *Pistacia*. For example, aphids identified as *G.utricularia* (Passerini, 1856), a species originally described from *Pistacia terebinthus* in Italy, occur commonly on roots of cereals and grasses in central and northern Europe and in North America. *G.utricularia* presents a particularly difficult taxonomic problem. The name *G.utricularia* has been applied to all populations with numerous short, dispersed hairs on the anal plate, but the root-feeding populations in Europe and North America vary greatly in other aspects of chaetotaxy (number of hairs on ultimate rostral segment, eighth abdominal tergite, cauda, presence or absence of spatulate hairs), and karyotype (Blackman & Eastop, 1984).

Aphids currently regarded as *G.utricularia* occur on *Pistacia* species other than *P.terebinthus*. Populations on *P.mutica* in the Crimea and on *P.atlantica* in the Mediterranean area are currently regarded as a subspecies of *G.utricularia* (*muticae* Morvilko, 1928), and there are consistent electrophoretic differences perhaps indicative of sibling species, between populations of '*utricularia*' on *P.atlantica* and *P.palaestina* in Israel (Koach & Wool, 1977).

Thus the name *utricularia* is apparently being applied at present to a complex including species and subspecies on *Pistacia* and thelotokous (anholocyclic) races on cereals and grasses. Eastop & Hille Ris Lambers (1976) regarded *G.utricularia* as one member of 'a group of species not yet fully understood' and it is this *G.utricularia* group of species which is the main subject of this paper.

In this paper we report on a multivariate study of available samples of emigrant alatae to see whether these group according to the species of *Pistacia* from which they were collected. We recognize new *Geoica* species within the *utricularia* group, specific to *P.atlantica* and *P.palaestina*, and discuss the relation between the *Pistacia*-feeding generations and those on secondary host plants.

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Materials and Methods

The study was based on material from the following depositories: The Natural History Museum, London (BMNH); Israel National Insect Collection, Tel Aviv University (INIC), and the Museum National d'Histoire Naturelle, Paris (MNHN). Material studied for morphometric analyses consisted of alate emigrants from galls of known species of *Pistacia* from France, Italy, Morocco, Israel and Iran. Using the assumption that alatae inside one gall are the offspring of one fundatrix and so represent a single clone, up to ten specimens were measured from forty-four galls (378 specimens, Table 1) using a Kontron Videoplan interactive measuring system. Measurements were made according to the methods illustrated in Ilharco & van Harten (1987). Eighteen characters used previously in the taxonomy of *Geoica* were selected (Table 2) and measured for each specimen (Davatchi & Remaudière, 1957; Wool & Koach, 1976; V. F. Eastop, unpublished data).

To investigate host-related differences in general morphology, canonical variate analyses (CVA) were carried

Table 1. Samples of *Geoica utricularia* species group measured.

Sample no.	Host	Locality	Date	No. of measured specimens: Migrants	No. of measured specimens: Exules	Karyotype
DHRL F87	*P.terebinthus*	France	19.ix.1959	10	8 (grass)	
DHRL F89	*P.terebinthus*	France	25.ix.1959	10		
Leclant 727	*P.terebinthus*	France	4.viii.1964	7		
Feltwell 19281	*P.terebinthus*	France	viii.1981	4		
DHRL 833	*P.terebinthus*	Italy	22.ix.1973	10		
DHRL 836	*P.terebinthus*	Italy	22.ix.1973	10		
DHRL 837	*P.terebinthus*	Italy	22.ix.1973	10		
VFE 14330	*P.terebinthus*	Italy	x.1973	10		
VFE 14331	*P.terebinthus*	Italy	x.1973	6		
Tremblay	*P.terebinthus*	Italy	x.1973	–	2	
RLB 1467	*P.terebinthus*	Sicily	20.x.1977	4		2n = 18
RLB 1911	*P.terebinthus*	Crete	16.viii.1979	–		2n = 21
Talhouk 57	*P.terebinthus*	Lebanon	1.xi.1972	10		
Bodenheimer	*P.palaestina*	Israel	20.x.1949	5		
Remaud. 1669	*P.palaestina*	Cyprus	24.x.1962	10		
DHRL 844	*P.palaestina*	Israel	5.xi.1973	10		
DHRL 845	*P.palaestina*	Israel	5.xi.1973	10	5	
RLB 155	*P.palaestina*	Israel	13.xi.1974	5		
RLB 157	*P.palaestina*	Israel	13.xi.1974	9		2n = 18?
RLB 160	*P.palaestina*	Israel	13.xi.1974	10		2n = 18
RLB 161	*P.palaestina*	Israel	13.xi.1974	7		
RLB 164	*P.palaestina*	Israel	13.xi.1974	10		2n = 18
RLB 167	*P.palaestina*	Israel	13.xi.1974	10		2n = 18?
Davatchi P36	*P.mutica*	Iran	ix.1957	6		
Remaud. i673	*P.mutica*	Iran	28.vi.1955	10 + 10		
Remaud. i1173	*P.mutica*	Iran	20.vi.1955	8		
Remaud. i1261	*P.mutica*	Iran	20.x.1955	6		
Remaud. 0492a	*P.atlantica*	Morocco	24.x.1954	4		
Remaud. 0965a	*P.atlantica*	Morocco	ix.1957	10 + 7		
Remaud. 0965b	*P.atlantica*	Morocco	ix.1957	10		
Remaud. 0988a	*P.atlantica*	Morocco	28.ix.1957	5		
Remaud. 0988c	*P.atlantica*	Morocco	28.ix.1957	10		
Remaud. 0988f	*P.atlantica*	Morocco	28.ix.1957	10 + 10		
VFE 14332	*P.atlantica*	Israel	x.1973	10		
RLB 158	*P.atlantica*	Israel	12.x.1974	10		
RLB 163	*P.atlantica*	Israel	12.x.1974	10		2n = 18?
RLB 168	*P.atlantica*	Israel	12.x.1974	10		
DHRL 838	*P.atlantica*	Israel	4.x.1973	10		
DHRL 839	*P.atlantica*	Israel	4.x.1973	10		
DHRL 842	*P.atlantica*	Israel	4.x.1973	10		
DHRL 843	*P.atlantica*	Israel	4.x.1973	10		
DHRL 862	*P.atlantica*	Israel	12.x.1974	5		
VFE 14333	*P.atlantica*	Israel	x.1973	10		
RLB 162	*P.atlantica*	Israel	12.x.1974	10		

Table 2. Morphological characters of *Geoica utricularia* species group measured for biometric analyses.

1. Body length
2. Head width
3. Length of antennal segment 3 (AS3)
4. Length of antennal segemtn 4 (AS4)
5. Length of antennal segemtn 5 (AS5)
6. Length of base of antennal segment 6 (AS6)
7. Length of terminal process of anternna (PT)
8. Length of ultimate rostral segment (URS)
9. Length of hind tibiae (HTIB)
10. Length of hind tarsal segment 2 (HT2)
11. Length of longest lateral hair on embryo (EMLAT)
12. No. of secondary rhinaria on antennal segment 3 (RH3)
13. No. of secondary rhinaria on antennal segment 4 (RH4)
14. No. of secondary rhinaria on antennal segment 5 (RH5)
15. No. of secondary rhinaria on antennal segment 6 (RH6)
16. No. of hairs on fourth tergite of embryo (EMT)
17. No. of hairs on dorsum of hind tarsal segment 2 (HT2D)
18. No. of hairs on venter of hind tarsal segment 2 (HT2V)

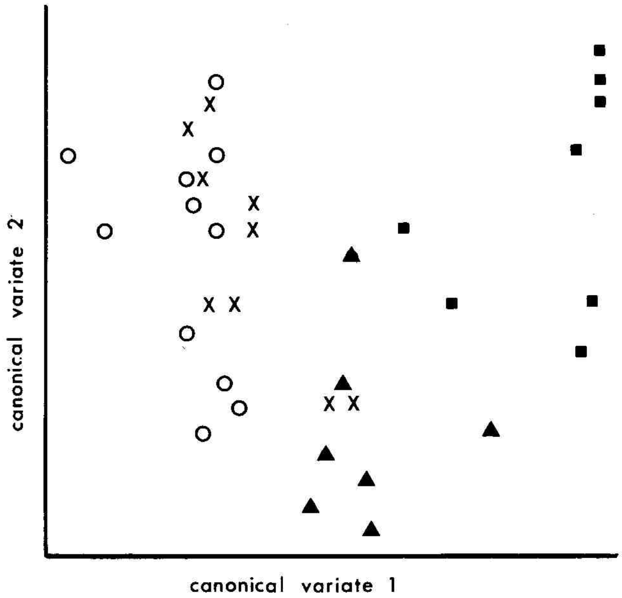

Fig. 1. Plot of the mean scores on the first two canonical variates for samples of emigrant alatae from galls from identified species of *Pistacia*. Samples from *P.terebinthus* (open circles); samples from *P.palaestina* (crosses); samples from *P.atlantica* (black symbols) provisionally identified as *Geoica rungsi* (triangles) and *G.harpazi* (squares).

out, with the untransformed data grouped by individual galls. The use of clones (in this case individual gall populations) as the groups in CVA has been shown to be a powerful method for the discrimination of taxa in aphids (Blackman, 1992). It has the considerable advantage of being a completely objective approach that in no way prejudices the subsequent ordination of the group, overcoming a common criticism of the use of CVA in systematic studies (Thorpe, 1983). The CVA program was a version of Blackith & Reyment (1971), written in BASIC by I. M. White. Characters contributing most to the separation of putative taxa were tested in bivariate plots (using Technicurve from Aston Scientific), and the best discriminant combinations were computed as simple ratios.

Results and Discussion

Canonical variates analysis

Mean scores of the first two canonical variates (CV1 and CV2) show some tendency to form clusters, CV1 scores in particular having some relation to the host plant (Fig. 1). Samples from *P.terebinthus* (*utricularia* sensu stricto) all had lower scores on CV1 than those from *P.atlantica*. Of the *P.atlantica* samples, those from Israel and Morocco previously identified as *G.rungsi* separated from those from Israel to which Hille Ris Lambers had allotted the manuscript name *harpazi*. *Geoica harpazi* has a number of unique characters and is clearly a distinct species (see later description), so it was excluded from subsequent analyses. Aphids from *P.palaestina* grouped mostly with those from *P.terebinthus*. CVs 3–5 failed to provide any significant clusters.

When five samples from *P.mutica* from Iran were included in the CVA, one sample appeared among the *terebinthus* material (i673a collected in June), whereas the other samples (including i673m collected at the same time from a different gall) had CV1 scores similar to samples from *P.atlantica* (Fig. 2). However, a CVA that included only the *P.atlantica* and *P.mutica* samples provided CV1 scores that separated the alatae from these two hosts (Fig. 3).

Taxa within the Geoica utricularia group

The CVA results failed to give very discrete groupings but were nevertheless indicative of host-related differences between the populations. Further study was therefore undertaken to delineate taxa and identify possible discriminants. It was postulated that at least five taxa (and possibly a sixth) exist within the *G.utricularia* group on *Pistacia* in the western Palearctic.

***Geoica utricularia* (Passerini)** (Figs 4c, 6c)

Pemphigus utricularia Passerini, 1856: 206.
Tychea eragrostidis Passerini, 1860: 39.
Tychea setariae Passerini, 1860: 40.
Pemphigus utriculoides Lichtenstein, 1880: 3.
Endeis carnosa Buckton, 1883: 92.
Endeis pellucida Buckton, 1883: 91.
Geoica squamosa Hart, 1894: 102.
Geoica cyperi Schouteden, 1902: 138.
Geoica discreta Börner, 1952: 203.

Emigrants from *P.terebinthus* (Tables 3 and 4) mostly have a shorter AS3 than other populations (Fig. 4c), and

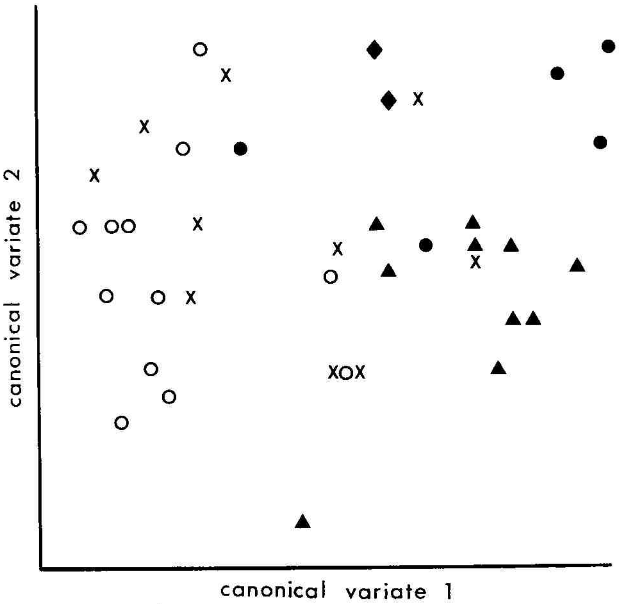

Fig. 2. Plot of the mean scores on the first two canonical variates for samples of emigrant alatae from galls from identified species of *Pistacia*, omitting *G.harpazi*. Samples from *P.terebinthus* (open circles); samples from *P.palaestina* (crosses); samples from *P.atlantica* (triangles); samples from *P.mutica* (black circles) and two atypical samples from *P.atlantica* from Morocco, 0998a and c (diamonds).

this gives some discrimination using ratios or bivariate plots involving AS4, AS6, Htib and HT2 (Table 3 and Fig. 7). The embryos within them have relatively few (16–30) hairs on the anal plate (Fig. 6c), a character

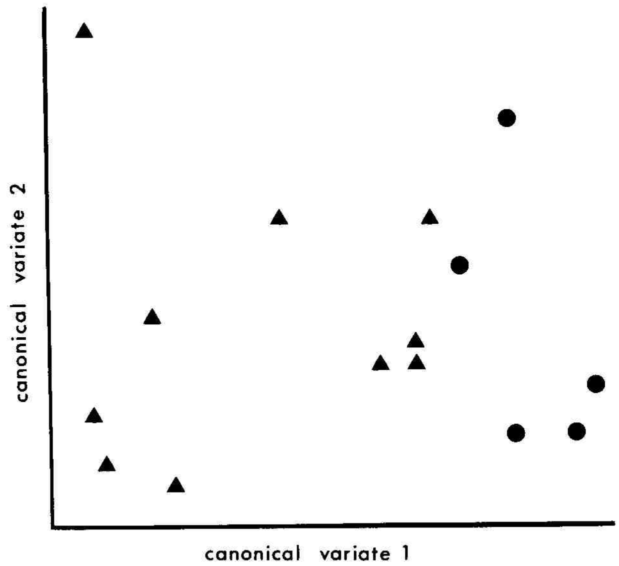

Fig. 3. Plot of the mean scores on the first two canonical variates for samples of emigrant alatae from galls from *Pistacia atlantica* (black triangles) and *P.mutica* (black circles).

Table 3. Range of variation (in mm) and means (in parentheses) recorded for morphological characters of emigrant alatae of *Geoica utricularia* species group on different *Pistacia* species.

			Length of antennal segments							Secondary rhinaria				Hair numbers			Hair length
Pistacia host/ *Geoica* species	No. measured	Body length	AS3	AS4	AS5	AS6 + PT	Length URS	Length HTIB	Length HT2	AS3	AS4	AS5	AS6	HT2	Embryo tergite	Embryo anal plate	(µm) embryo tergite
ex *P.terebinthus utricularia* ss.	92	1.4–2.7 (2.02)	0.17–0.27 (0.19)	0.09–0.16 (0.12)	0.08–0.13 (0.10)	0.10–0.16 (0.13)	0.09–0.11 (0.10)	0.47–0.74 (0.59)	0.13–0.19 (0.15)	7–30 (17)	2–14 (8)	0–9 (3)	0–3 (0.6)	4–16 (8)	7–14 (10)	20–30 (25)	29–58 (38)
ex *P.atlantica rungsi*	90	1.2–2.1 (1.73)	0.16–0.27 (0.22)	0.09–0.14 (0.11)	0.08–0.11 (0.09)	0.09–0.13 (0.12)	0.08–0.10 (0.09)	0.38–0.59 (0.50)	0.11–0.16 (0.13)	11–30 (18)	3–10 (7)	0–8 (2)	0–3 (0.8)	4–13 (7)	6–22 (10)	30–60 (49)	32–70 (47)
ex *P.atlantica mutica muticae*	40	1.8–2.5 (2.14)	0.14–0.32 (0.25)	0.09–0.18 (0.13)	0.08–0.14 (0.10)	0.09–0.15 (0.12)	0.09–0.12 (0.11)	0.49–0.65 (0.57)	0.12–0.18 (0.15)	13–45 (24)	4–17 (9)	0–11 (4)	0–6 (2.5)	6–14 (11	7–12 (8)	16–25 (20)	40–58 (47)
ex *P.atlantica harpazi* n.sp.	65	1.6–2.4 (1.92)	0.17–0.26 (0.21)	0.09–0.14 (0.12)	0.08–0.11 (0.10)	0.10–0.14 (0.12)	0.08–0.10 (0.09)	0.36–0.54 (0.45)	0.12–0.16 (0.14)	6–23 (11)	1–11 (4)	0–5 (1)	0–2 (0.2)	10–21 (16)	12–26 (20)	35–64 (45)	28–78 (52)
ex *P.palaestina wertheimae* n.sp.	86	1.5–2.8 (2.15)	0.18–0.29 (0.22)	0.10–0.15 (0.12)	0.08–0.13 (0.10)	0.10–0.17 (0.13)	0.08–0.12 (0.10)	0.45–0.66 (0.56)	0.12–0.18 (0.15)	12–33 (19)	4–13 (7)	0–8 (3)	0–3 (0.7)	7–14 (10)	6–15 (10)	36–69 (42)	27–60 (39)
ex *P.atlantica* 0988 a + c	15	1.9–2.8 (2.31)	0.24–0.27 (0.25)	0.11–0.15 (0.13)	0.10–0.13 (0.11)	0.11–0.14 (0.12)	0.11–0.14 (0.12)	0.67–0.79 (0.71)	0.16–0.20 (0.18)	16–23 (19)	4–9 (7)	1–5 (3)	1–2 (1.1)	8–15 (11)	8–10 (9)	36–57 (47)	80–120 (104)

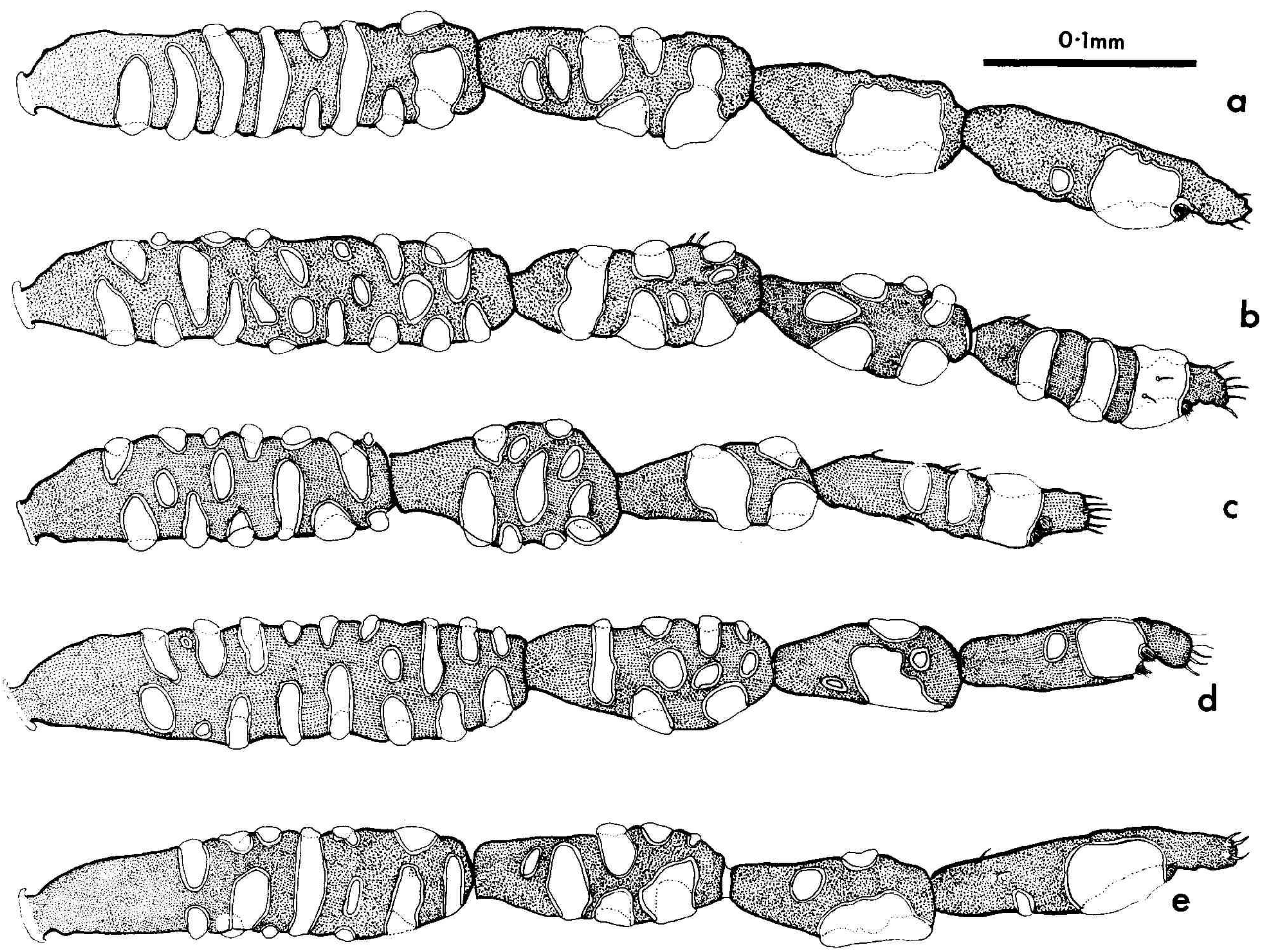

Fig. 4. Antennal segments 3–6 of emigrant alatae: a, *Geoica harpazi*; b, *G.rungsi*; c, *G.utricularia*; d, *D.muticae*; and e, *G.wertheimae*.

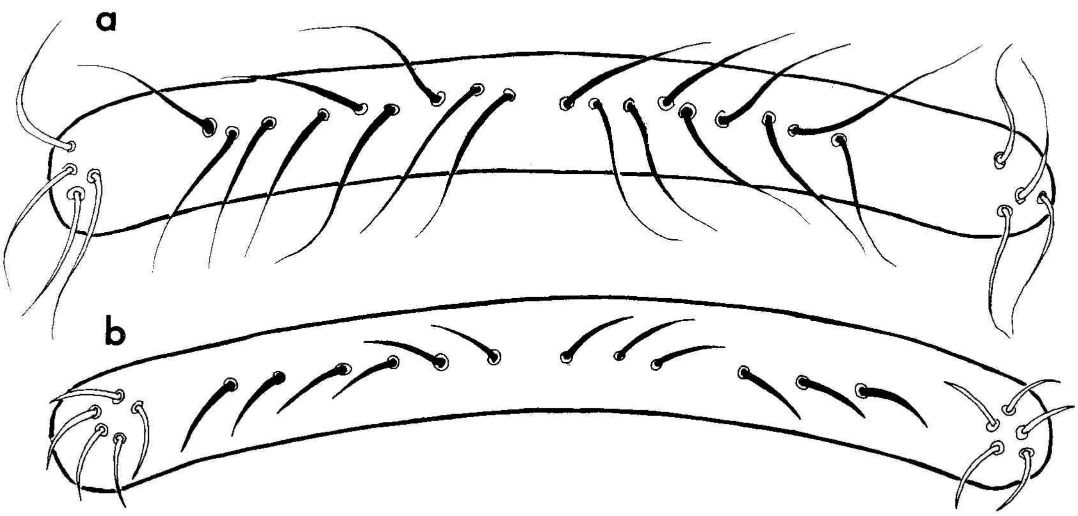

Fig. 5. Hairs on third abdominal tergite of embryos within emigrant alatae of a, *Geoica harpazi*; b, *G.wertheimae*.

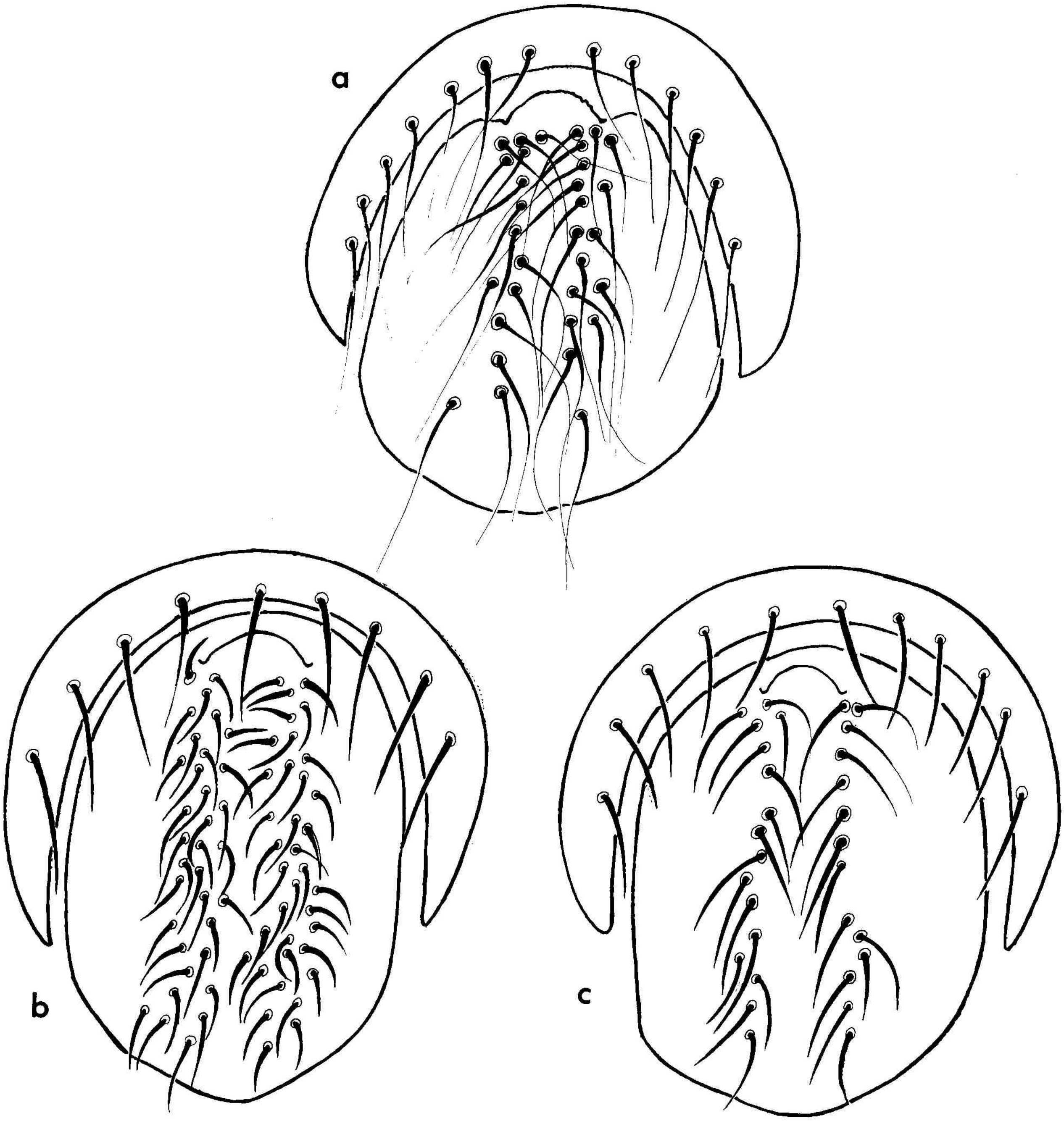

Fig. 6. Abdominal tergite 8 and anal plate of embryos within emigrant alatae of a, *Geoica harpazi*; b, *G.wertheimae*; c, *G.utricularia*.

shared only with emigrants from *P.mutica*, compared with 30–69 hairs in other populations (Figs 6a, b). *G.utricularia* was described by Passerini from *P.terebinthus* and we consider that it only colonizes this *Pistacia* species. The range of *P.terebinthus* extends throughout the northern Mediterranean area and alate emigrants that can definitely be assigned to *G.utricularia* have so far been identified from France, Italy and Lebanon. Passerini did not designate type material, but two tubes without data were located within the Passerini collection at the Museo di Storia Naturale e Laboratorio at Parma, Italy (tubes 155 and 156) and the aphids were slide mounted and designated as the lectotype series of *Pemphigus utricularius* Passerini. Roberti (1939, 1983) provided detailed accounts of all morphs of this species in Italy.

Table 4. Discriminant ratios recorded for morphological characters of emigrant alatae of the *Geoica utricularia* species group from different *Pistacia* species.

Pistacia host/ *Geoica* species	No. measured	Antennal flagellum/ body length	AS4/AS6	HTIB/BL	AS4/HT2	HTIB/AS3	AS3/HT2	URS/HT2
ex *P.terebinthus utricularia* ss.	92	<0.28 60%	<1.0 87%	≥0.25 93%	<0.82 90%	<2.5 91%	<1.5 94%	<0.63 55%
ex *P.atlantica rungsi*	92	<0.28 92%	<1.0 70%	≥0.25 92%	≥0.82 94%	≥2.5 95%	≥1.5 89%	>0.63 94%
ex *P.mutica muticae*	40	≥0.28 80%	<1.0 75%	≥0.25 82%	≥0.82 66%	≥2.5 70%	≥1.5 80%	>0.63 90%
ex *P.atlantica harpazi* n.sp.	65	≥0.28 77%	≥1.0 75%	<0.25 77%	≥0.82 92%	<2.5 100%	<1.5 55%	>0.63 92%
ex *P.palaestina wertheimae* n.sp	86	<0.28 73%	≥1.0 92%	≥0.25 60%	<0.82 80%	≥2.5 55%	≥1.5 66%	>0.63 80%
ex *P.atlantica* 0988 a + c	15	<0.28 60%	≥1.0 92%	≥0.25 100%	<0.82 100%	≥2.5 100%	<1.5 100%	>0.63 65%

***Geoica muticae* (Mordvilko)** (Fig. 4d)

Pemphigetum muticae Mordvilko, 1928: 525.
Geoica utricularia subsp. *muticae* Mordvilko, 1929: 64.

Mordvilko (1928) described *Pemphigetum muticae* from galls on *P.mutica* in the Crimea and in 1929 he relegated it to suspecific status within *utricularia*. We have examined seven specimens of emigrant alatae from Mordvilko's type series, collected on 1 August 1928, and compared them with Iranian samples collected in June and September–October (Tables 3 and 4). *G.muticae* resembles *utricularia* in having embryos with less than 30 hairs on the anal plate, but AS3 is usually shorter, especially in those emerging from galls on *P.mutica* at the same time as those of *G.utricularia* on *P.terebinthus* in September–October

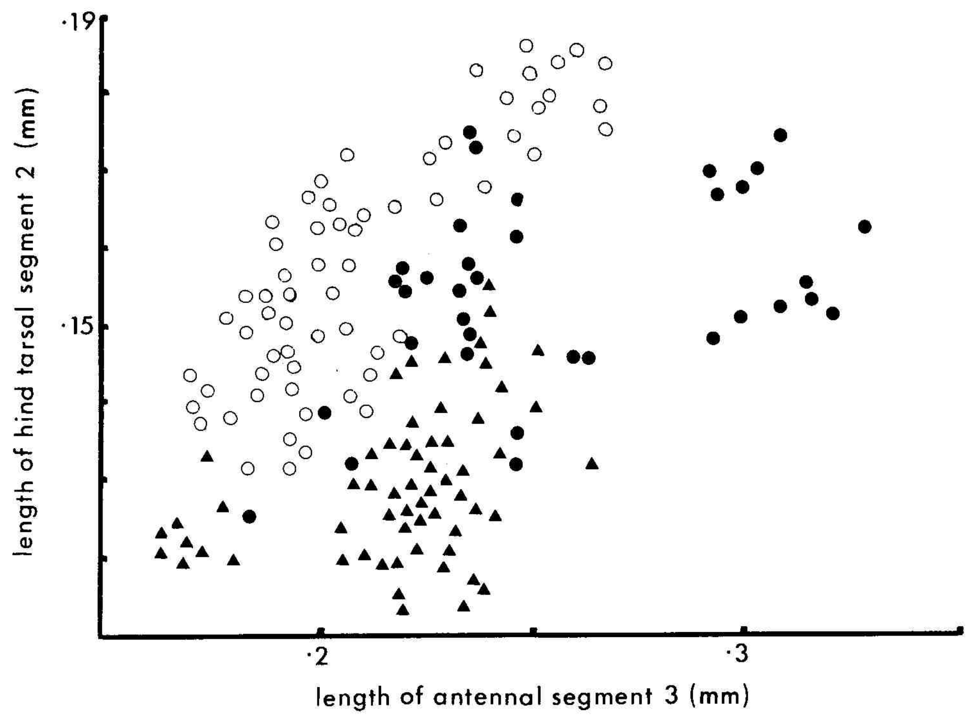

Fig. 7. Bivariate plot of the lengths (in mm) of the third antennal segment against the second segment of the hind tarsus for individual emigrant alatae of *Geoica utricularia* (open circles), *G.rungsi* (triangles) and *G.muticae* (filled circles).

(Fig. 4d, and right-hand cluster in Fig. 7). However, there is significant seasonal variation in this species, as two samples (i673a and m) collected from galls in June (unusually early for a *Geoica* species) had (i) fewer secondary rhinaria, (ii) a more *utricularia*-like shorter AS3 (Fig. 7), (iii) AS6 longer than AS4, and (iv) CV1 scores were closer to *utricularia* (Fig. 2). Mordvilko (1928) noted that galls on *P.mutica* in southern Russia opened in July, so early maturation of alatae may be a regular feature of this species. Mordvilko's specimens collected on 1 August also had a rather short AS3, but the ratio of AS3 to Htib discriminated them from *utricularia*. Mordvilko (1935) compared AS3 with AS6 to discriminate between *muticae* and *utricularia*, but we found this ratio of no use for this purpose (Table 4). *P.mutica* occurs in Central Asia from Turkey to Afghanistan.

Geoica rungsi Davatchi & Remaudière (Fig. 4b)

Geoica utricularia subsp. *rungsi* Davatchi & Remaudière, 1957: 176; Eastop & Hille Ris Lambers, 1976: 204 (= *muticae*).

Davatchi & Remaudière (1957) described *rungsi* as a subspecies of *G.utricularia* on galls on *P.atlantica* in Morocco and Israel. Many samples of *rungsi* including type material in the BMNH collection and loaned from G. Remaudière were measured (Tables 3 and 4). Emigrants from galls on *P.atlantica* in Israel and Morocco contained embryos with 30–60 hairs on the anal plate as compared to 16–30 in *utricularia* or *muticae*. These embryos had 6–22 (mean 10) short hairs on each abdominal tergite, which were similar in number and form to the embryonic hairs of *utricularia* and *muticae*, but unlike the long, attenuated and often more numerous hairs of the embryos of *harpazi* (12–26, mean 20; Fig. 5a). The specimens of *rungsi* tended to be smaller than those of other populations making morphometric comparison more difficult. However, *rungsi* had a relatively shorter HT2 and AS6 than *utricularia* (Figs 7 and 8), and the HTib/AS3 ratio was also discriminatory (Tables 3 and 4). However, specimens collected in Iran by Remaudière on *P.mutica* consistently have fewer hairs on the embryonic anal plate than *rungsi*. Total flagellum length/body length also provides some discrimination, 92% of *rungsi* had this ratio greater than 0·28 and 80% of *muticae* had this ratio less than 0.28 (Table 4).

Eastop & Hille Ris Lambers (1976) synonymized *rungsi* with *muticae* which would seem reasonable following Rechinger's (1969) designation of *Pistacia mutica* as being a subspecies of *atlantica*. The results of the above analysis led us to remove *rungsi* from synonymy with *muticae*.

Characters used by Davatchi (1958) to separate *G.rungsi* and *muticae* from *utricularia* do not discriminate satisfactorily specimens studied here; according to Davatchi HT2 is at least 1.6 times longer than URS in *G.utricularia*, but this was true of only 56% of the individuals that we measured from *P.terebinthus* (Table 4). Also, there was too much overlap of the lengths of the longest hairs on HT1 for their use in discrimination. Davatchi (1958) recorded 9–16 secondary hairs on HT2 in *muticae* and 4–8 in *rungsi*

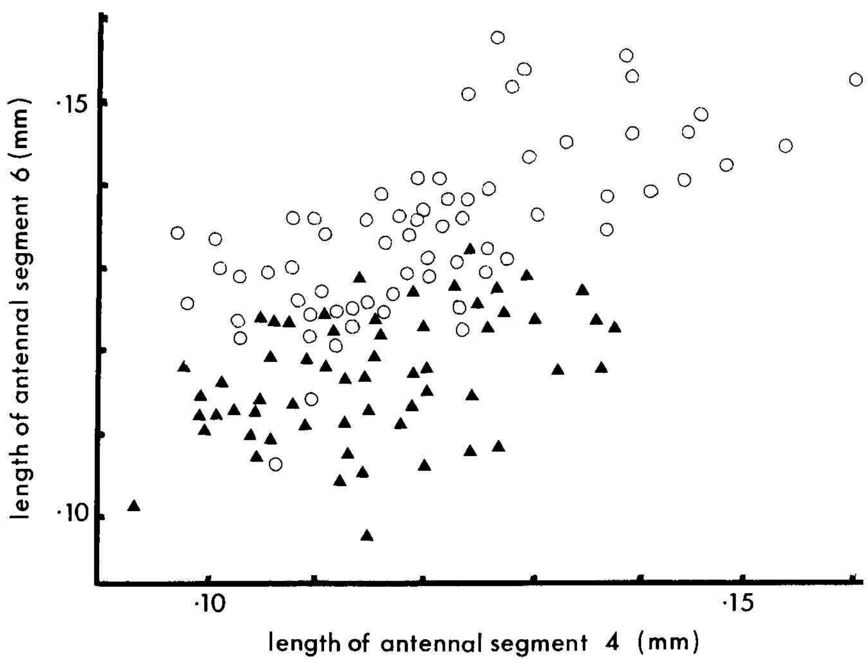

Fig. 8. Bivariate plot of the lengths (in mm) of the fourth antennal segment against the sixth antennal segment for individual emigrant alatae of *G.utricularia* (circles) and *G.rungsi* (triangles).

in Iran, but we found that the number of secondary hairs on HT2 did not vary much between all the samples studied, and did not exceed 10 in number even for the Iranian material (Davatchi P36, Table 1). We have not checked his observations, so we cannot be certain whether his material differs from our own. The range of *P.atlantica* is from Israel to the Canary Islands, throughout the north African Sahara region.

Two of Remaudière's samples within the paratype series of *rungsi* from *P.atlantica* from Morocco (0988 a and c) comprised larger specimens with relatively long URS and HT2, and containing embryos with dorsal hairs which are stout basally and attenuated apically and 80–120 μm long, as compared with 32–70 μm in *rungsi* and 28–70 μm in *harpazi*, as well as a few shorter spatulate hairs. There two samples grouped together in CVA plots, perhaps partly because of their larger size (Fig. 2). More samples are needed to decide whether these populations warrant separate species status.

G.wertheimae sp.n. (Tables 3 and 4; Figs 4e, 5b, 6b).

Alate emigrant (86 specimens measured from ten galls).

Body 1.5–2.8 mm long, 3.0–4.3 times length of hind tibiae. Antennal segment ratios for AS3–6 22:12:10:11+2. Secondary rhinaria subcircular and/or forming transverse bars, usually less than half circumference of segment (Fig. 4e); AS4 usually less than 0·82 times length of HT2 (80% of measured specimens). AS6 (including PT) usually shorter than AS4 (92% of measured specimens). URS 0.5–0.7 times length of HT2 and bearing 4–8 secondary hairs. Htib 0.2–0.3 times body length. First tarsal chaetotaxy 3:3:3. HT2 with 7–14 (mean 10) secondary hairs: 2–7 dorsal and 3–9 ventral. Abdomen with marginal wax glands multifaceted and variable in size. Dorsal wax glands single-faceted if present. Sclerotic band variably present on seventh sternite.

Embryo apterous exule within alate emigrant. Embryos with 6–15 stout hairs, 27–60 μm (mean 39 μm) long on each abdominal tergite (Fig. 5b) and 36–60 similar hairs on anal plate (Fig. 6b).

Apterous exule (five specimens measured, exules from emigrant alatae from galls on *Pistacia palaestina*, ex culture *Poa annua*).

Body length 1.31–1.59 mm. Antennae 5-segmented, AS3 0.14–0.19 mm, AS4 0.07–0.09 mm, AS5 0.08–0.10 mm, PT 0.02–0.03 mm, URS 0.17–0.18 mm, 1.35–1.87 times HT2 with 7–10 secondary hairs; Htib 0.35–0.43 mm; Hfem 0.32–0.43 mm; HT2 0.10–0.13 mm with 3–4 secondary hairs. Body hairs variable: stout and pointed, strap-like, bifurcate and palmate, sometimes arising from small sclerites. Tergites variably sclerotic with some reticulation. Hair number on tergite VIII 16–25. Wax glands small or absent.

Type material

Holotype. ISRAEL: Jerusalem, 5.xi.1973 (*Wertheim*, HRL 845), alate emigrant from gall of *Pistacia palaestina* (BMNH).

Paratypes. ISRAEL: Jerusalem, 5.xi. 1973 (*Wertheim*, HRL 844, 845), 33 alate emigrants ex *Pistacia palaestina*, 5 apterous exules ex *Poa annua* from *Pistacia palaestina*, ex culture (HRL 845). Beth Hake-em 20.x.1949 (*Boddenheimer*), 12 alate emigrants ex *Pistacia palaestina*. Ora Junction, 13.x.1974) *Hille Ris Lambers*, RLB 155, 157, 160, 161, 164, 167), 56 alate emigrants ex *Pistacia palaestina*. CYPRUS: Khrysor, 24.x.1962 (*Remaudière* 1669), 12 alate emigrants ex *Pistacia palaestina*. LEBANON, 18.viii.1959 (*Remaudière* 1597), 3 alate emigrants ex *Pistacia palaestina* (BMNH, INIC, MNHN).

Comments

Hille Ris Lambers recognized and gave a manuscript name to this species from *P.palaestina* in Israel. Samples measured clustered mainly with *utricularia* in CVA, but overlapped somewhat with *rungsi*. Morphometric characters were mostly intermediate between *utricularia* and *rungsi*. They can be separated from *utricularia* by the chaetotaxy of the embryonic anal plate, but discrimination from *rungsi* is more difficult; only the ratio of AS4/HT2 gives over 80% discrimination (Fig. 8 and Table 4).

Wool & Koach (1976) compared emigrants from *P.atlantica* and *palaestina* at nine collection sites in Israel using paired-comparison *t* tests. They found that only two out of nineteen characters showed significant differences (thorax width and length of AS4). They considered this to be 'type 1 error' and assumed that the aphids on the two hosts did not differ when sampled in the same locality. However, a difference in AS4 was also demonstrated in the present work as the ratio of AS4/HT2 (Fig. 9), and indicates that *wertheimae* and *rungsi* are consistently different in this respect. One can conclude that no populations of *harpazi* were included in their collections from *P.atlantica* at that time, as its distinctive characters would have been obvious in the statistical analysis.

Koach & Wool (1977) also demonstrated a difference in esterase mobility between samples from *P.atlantica* and *P.palaestina*. One can presume on morphological grounds that the material from *atlantica* in their electrophoretic study was *rungsi* and not *harpazi*, so it appears that there is a consistent esterase difference between *wertheimae* and *rungsi*, which further confirms their status as separate species. *G.wertheimae* is referred to as species 'B' in Halperin *et al.* (1988), but because of a mistake made in correspondence, the host was wrongly stated as being *atlantica*. The range of *P.palaestina* is localized in the Eastern Mediterranean region.

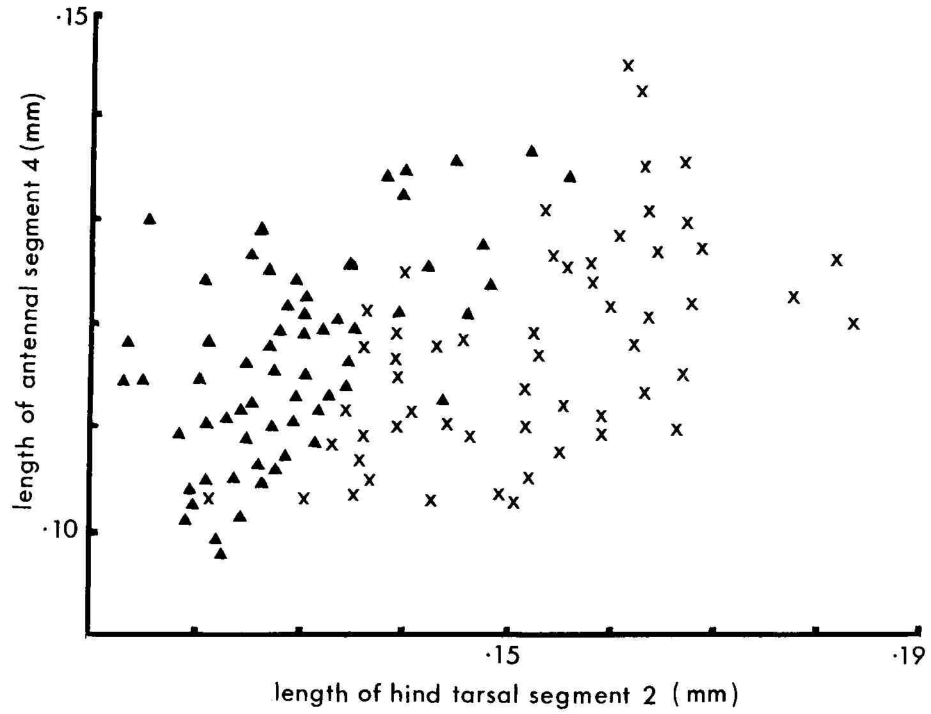

Fig. 9. Bivariate plot of the lengths (in mm) of the fourth antennal segment against the second segment of the hind tarsus for individual emigrant alatae of *G.wertheimae* (crosses) and *G.rungsi* (triangles).

***Geoica harpazi* sp.n.** (Tables 3 and 4; Figs 4a, 5a, 6a)

Alate emigrant (65 specimens measured from seven galls).

Body 1.62–2.4 mm long, 3.6–4.6 times length of hind tibiae. Antennae 6-segmented (Fig. 4a). Antennal segment ratios for AS3–6 20:10:9:9+2. Secondary rhinaria forming transverse bands about half circumference of segment; variable in size, those on AS5 and AS6 either small and distinct or large and coalescing into primary rhinaria; 2–4 small subsidiary and heavily ciliated rhinaria distal to primary rhinaria on AS6. Base of AS6 with 15–25 hairs. URS 0.6–0.8 times length of HT2 and bearing 6–10 secondary hairs. Htib 0.2–0.3 times body length. First tarsal chaetotaxy 3:3:3. HT2 with 10–21 (mean 16) secondary hairs; 6–12 dorsal and 4–10 ventral.

Abdomen with large round spiracles surrounded by small sclerites. Wax glands present on dorsum and margins, marginal glands with 5–15 facets and similar in size to marginal sclerites, dorsal glands few and of one facet only. Subgenital and subanal plates, gonapophyses, tergites 7 and 8 sclerotized, and a variably present sclerotic band on sternite 7. Abdominal hairs on non-sclerotic areas short and difficult to detect, being masked by the more obvious long hairs of the embryos; hairs on sclerotic areas attenuated but not as long as the embryonic hairs.

Embryo apterous exule within alate emigrant. Embryos with rows of 14–30 very long, attenuated and wavy hairs on abdominal tergites (Fig. 5a) and 35–64 long, attenuated hairs on dorsally displaced anal plate (Fig. 6a). Similar hairs on antennae, rostrum and legs.

Apterous exule (13 specimens measured, exules from emigrant alatae from galls on *Pistacia atlantica*, ex culture *Poa annua*).

Body 1.70–2.61 mm. Antennae 5-segmented, antennal segment ratios for AS3–5 9:5:5:1; AS3 0.15–0.21 mm, AS4 0.07–0.11 mm, AS5 0.08–0.12 mm, PT 0.2–0.35 mm. Small but heavily ciliated primary rhinaria on AS4 and AS5. Eye with three ommatidia. URS 0.20–0.26 mm; 0.10–0.14 times length of body and 1.6–1.9 times length of HT2. Number of secondary hairs on URS 16–30. HT2 0.10–0.16 mm with 9–15 secondary hairs. Hind femora 0.43–0.70 mm; Htib 0.46–0.58 mm. Hairs on body long and attenuate, in particular on posterior tergites and on dorsally displaced anal plate, some spatulate hairs variably present. Eighth abdominal tergite with 50–100 hairs, and at least 100–200 hairs on the dorsally prolonged and rectangular anal plate. Abdomen with sclerotized bands on abdominal tergites 7 and 8; sclerotized anal plate, gonapophyses and subgenital plate; and small round sclerites surrounding the large round spiracles. Wax glands not usually present. (N.B. One sample collected in February (Halperin 62) has tergites more heavily sclerotized, with wax glands and with many spatulate hairs on the dorsum.)

Apterous fundatrigenia (10 specimens measured from two galls on *Pistacia atlantica*, HRL 842 and 862).

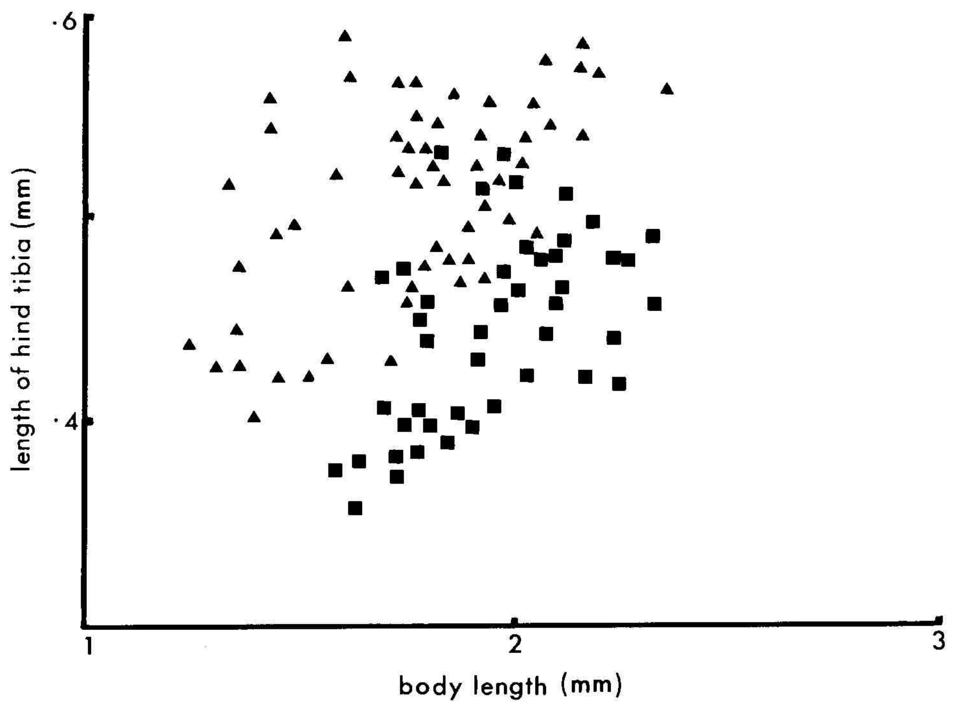

Fig. 10. Bivariate plot of the lengths (in mm) of body against hind tibia for individual emigrant alatae of *G.rungsi* (triangles) and *G.harpazi* (squares).

Body 1.12–1.42 mm. Antennae 5-segmented, 0.29–0.32 mm long and 0.25–0.31 times body length. Antennal segment ratios AS3-PT, 6:3:4:1; AS3 0.29–0.38 mm, AS4 0.09–0.12 mm, AS5 0.07–0.08 mm, PT 0.01–0.02 mm; AS4 0.92–1.25 times length of AS2 which is 0.04–0.06 mm; AS3 1.38–1.74 times length of AS5. Measurements of one specimen with 6-segmented antennae 0.51 mm long; AS3 0.15 mm, AS4 0.08 mm, AS5 0.07 mm, AS6 0.10, PT 0.02 mm. Rostrum length 0.26–0.30 mm, 0.6–0.92 times antennal length and 0.21–0.25 times body length; URS 0.10–0.12 mm, 1.73–1.96 times width at base, 1.89–2.20 times AS2 and 0.92–1.22 times HT2. HTIB 0.21–0.34 mm. HT2 0.09–0.10 mm. Cuticle uniformly pale, marginal and dorsal wax glands multifaceted, forming rows across each tergite. Small anal plate, cauda, gonapophyses and subgenital plate unsclerotized. Small sclerites associated with each spiracle. Hairs short but attenuated.

Alate sexupara (4 specimens collected from *Pistacia atlantica* and 5 from *P.palaestina*. The latter specimens presumably had alighted on the wrong host).

Body 1.5–2.16 mm. Antennae 5 or 6 segmented, 0.61–0.73 mm long and 0.32–0.34 times body length. Antennal segment ratios AS3–PT, 8:6:6:5:1; AS3 0.13–0.19 mm, AS4 0.10–0.14 mm, AS5 0.10–0.14 mm, AS6 0.10–0.12 mm, PT 0.02–0.03 mm. AS3 0.86–1.25 times length of HT2 and AS4 0.62–0.86 times length of HT2. Secondary rhinaria on AS3 2–5, on AS4 1–3, on AS5 0–1, URS 0.21–0.23 mm, 1.27–1.47 times length of HT2. HT2 0.14–0.17 mm. Htib 0.58–0.78 mm, 0.30–0.35 times body length and 3.5–4.7 times length of AS3. Sclerotized bands and marginal sclerites on all abdominal tergites, and sclerotized gonapophyses, subgenital plate and dorsally displaced anal plate. All abdominal tergites, marginal sclerites and anal plate with many attenuated hairs, 60–140 on tergite VIII. No spatulate hairs on abdominal tergites or marginal sclerites.

Type material

Holotype. ISRAEL: Jerusalem, 4.x.1973 (*Wertheim*, gall number 6 DHRL 842), alate emigrant from gall of *Pistacia atlantica* (BMNH).

Paratypes. ISRAEL: Jerusalem, 4.x.1973 (*Wertheim*, DHRL 838, 839, 842, 843), 106 alate emigrants, 5 fundatrigenae and many first instars; Jerusalem, Agron Street, 12.x.1974 (*Wertheim*, DHRL 862, *Blackman* 162), 22 alate emigrants, 5 fundatrigenae and 30 first instars; Jerusalem, x.1973 (*Eastop* 14333), 19 alate emigrants; Hula Valley, 1973 (*Wool* 40108) 1 alate emigrant; Golan, 1973 (*Wool* 40109), 1 alate emigrant; Tel Aviv, Canada Park, 7.iv.1992 (*Wool*), 4 alate sexuparae, all ex *Pistacia atlantica*. Tel Aviv, Canada Park, 7.iv.1992, 21.iv.1992 and 5.v.1992 (*Wool*), 5 alate sexuparae, ex *Pistacia palaestina*. Gevath, 25.ii.1942 (*Wertheim*), 7 exules, ex *Triticum durum* roots; Al-giya, 13.iii.1951 (*Harpaz* 51001), 4 exules ex *Hordeum sativum*; Jerusalem, 1973–74 (*Wertheim* 842, 843, 862, 886), 60 exules ex culture on *Poa annua* from *Pistacia atlantica*; 6 exules, 13.ii.1974 (*Halperin* 62), K.Haim ex *Ammophila arenaria*; (BMNH, INIC, MNHN).

Comments

Recognized and given the manuscript name *harpazi* by Hille Ris Lambers, it is referred to as species 'A' by Halperin *et al.* (1988). When compared with other *Geoica* populations, *harpazi* has more hairs on the head, thorax, antennal segments and second tarsal segments of the emigrants, and many more distinctive, attenuated hairs on the tergites, anal plate and ultimate rostral segment of the embryos, immatures and the adult, apterous exules and alate sexuparae, but fewer, if any, spatulate hairs. The alate emigrants and sexuparae usually have fewer secondary rhinaria on AS3 and AS4 (except for sample number HRL 862 with 19–23 on AS3 and 8–11 on AS4), and the antennae and hind tibiae are usually shorter in relation to body length than in *rungsi* (Fig. 9) and most other members of the *G.utricularia* group. Emigrants of other species on *Pistacia atlantica*, *palaestina* and *terebinthus* all have fewer, stouter hairs in the embryos and exules and usually more secondary rhinaria in the alatae.

Studying the adult exules bred from alatae from the galls of identified *Pistacia* species, *harpazi* had more hairs on the ultimate rostral segment and abdominal tergite 8, many more hairs (80–200) on the anal plate and usually a longer hind femora than any other species. Exules of *rungsi*, and exules bred from alatae from *P.palaestina* galls, have 35–45 hairs on the anal plate, whereas the anal plates of those bred from *P.terebinthus* carry 15–25 hairs. These differences in hair number parallel those found in the embryos. There were insufficient individual exules bred from known *Pistacia* species or of known clonal lineage to conduct multivariate analyses or to be certain of any other differences.

Variation in the G.utricularia group

The results of this study indicate that there are discriminant features between populations on different *Pistacia* species indicative of separate taxa, but that there is also considerable intraspecific variation. Remaudière (pers. comm.) suggested that the date of gall maturation might effect the morphology of the emigrant alatae. Emigrants from galls on *P.mutica* in June examined in the present study had fewer secondary rhinaria and shorter AS3 and AS4 than other samples collected from galls in October.

Although D. Hille Ris Lambers (unpublished) conducted transfers to grasses with the progeny of emigrant alatae from galls on known *Pistacia* species, insufficient exules were bred to maturity, and insufficient generations were reared, to demonstrate the variation in morphology that could be caused by subterranean conditions. For example, variation in the number of spatulate hairs can occur between generations, or be induced environmentally. Paul (1977) noted seasonal variation in spatulate hairs in British *G.utricularia* populations, with more spatulate hairs in summer, and suggested that this might be a way of reducing water loss. Such variation makes it difficult to relate the morphology of parthenogenic populations permanently living on grass roots to that of holocyclic populations recently transferred from *Pistacia*. Hille Ris Lambers recognized some exules collected on *Ammophila* in February (Halperin 62) with spatulate hairs on the dorsum as being *harpazi*, as the marginal and anal plate hairs were long and attenuated. Later in the season the possibility exists that *G.harpazi* might produce exules with spatulate hairs and without any of the characteristic attenuated hairs.

The apterae of anholocyclic populations of the *G.utricularia* group in northern Europe have many more hairs on the anal plate, more akin to the *rungsi–wertheimae* populations, than to the geographically closer French and Italian *utricularia* populations. This might reflect the ancestry of the northern European populations, but an increase in the number of hairs could equally be associated with environmental factors. To study this problem further it would be necessary to rear several generations of exules on grass roots under different environmental conditions, and/or to use techniques such as karyotype analysis, DNA fingerprinting and enzyme electrophoresis.

Gall morphology

We have incomplete knowledge of the nature of the galls on different *Pistacia* species. Wertheim (1954) noted that *Geoica* galls on *P.palaestina* in Israel were yellowish pink, smooth-surfaced and regularly spherical in shape, whereas galls on *P.atlantica* were described as being green, wrinkled, unevenly surfaced and irregularly shaped. Photographs in Wool & Koach (1976) and Koach & Wool (1977) further indicate that galls on *P.palaestina* are larger and tend to grow on the leaflet petiole, whereas those on *P.atlantica* are smaller and grow on the leaflet base, although Plate 1(2) in Koach & Wool (1977) does not conform to this. The galls on *P.atlantica* that they illustrate are probably those of *rungsi*, for reasons stated above. The gall of *harpazi* is undescribed.

Mordvilko (1928) described galls of *G.muticae* on *P.mutica* from southern Russia as never growing larger than a hazelnut in size (1.5–1.8 cm in cross-section) and opening in July, whereas galls on *P.terebinthus* were described as bag-like and slightly cauliform, hazelnut to walnut in size (up to 4 cm in cross-section), growing from the leaflet bases and opening in September. Roberti's (1939) galls on *P.terebinthus* fit the latter description. [A gall on *P.khinjuk* illustrated by Koach & Wool (1977) is large, smooth and spherical, growing on the leaflet petiole and similar to those on *P.palaestina*, but larger; it could possibly be the gall of *G.setulosa*.]

Key to the emigrant alatae of the genus *Geoica*

This key includes some difficult separations that will be more reliable if applied to samples of 10–20 individuals rather than to single specimens.

1 Abdominal tergites 2–8 each with a sclerotized transverse band. Anal plate not connected to cauda. Primary rhinarium on antennal segment VI with a variable ring of cilia. Embryos without mouthparts. Ex *Pistacia terebinthus* and *atlantica*. (North Africa) .... *Geoica mimeuri* (Gaumont)

– Abdominal tergites 2–4 without sclerotic transverse bands. Anal plate extended dorso-laterally, joined with the cauda to form perianal ring. Primary rhinarium on antennal segment VI not ciliated. Embryos with mouthparts 2

2 AS3 with 3–7 large secondary rhinaria, usually in a single row. AS4 with 1–2 and AS5 with 0–1 secondary rhinaria (when antennae 6-segmented). Embryos with spatulate dorsal hairs 3

– AS3 with 8 or more secondary rhinaria, not in a single row and AS4 with at least 3 rhinaria (when antennae 6-segmented). Embryos with dorsal hairs pointed or attenuated or (rarely) spatulate 4

3 Abdominal sternite 7 with a narrow transverse band separate from anterior edge of subgenital plate. AS3 with at least 4 hairs, 8–15 μm long. Embryos with body length less than 0.7 mm, and with a transverse row of 6–8 spatulate spino-pleural hairs between long marginal hairs on abdominal tergites 1–7. Ex *Pistacia khinjuk* and *sinensis*? (Africa, Southern Europe and Asia)* .... *G.lucifuga* (Zehntner)

– Abdominal sternite 7 without a transverse band. AS3 with 0–2 hairs, 4–9 μm long. Embryos with body length more than 0.8 mm, and with a transverse row of 10 or more spatulate spino-pleural hairs between long marginal hairs on abdominal tergites 1–7. Ex *Pistacia khinjuk* (Europe, Turkey and Iran) .. .. *G.setulosa* (Passerini)

4 Embryos with 14–30 long attenuated hairs between similar marginal hairs on abdominal tergites 1–7 and 35–64 similar hairs on anal plate. Hind tibiae short, usually less than 0.25 times body length. AS3 with 6–23 secondary rhinaria (mean of 65 specimens = 11). Ex *P.atlantica* (Israel) .... *G.harpazi* **sp.n.**

– Embryos with 6–17 long but stout pointed hairs between similar marginal hairs on abdominal tergites 1–7 and 16–29 similar normal hairs on anal plate. Hind tibiae longer, often more than 0.25 times body length. AS3 with 7–39 secondary rhinaria (mean of 310 specimens = 19) 5

5 Embryos with 16–30 hairs on anal plate forming a double row 6

– Embryos with 30–69 hairs on anal plate forming four rows or a broad band. Ex *P.atlantica* and *palaestina* 7

6 AS3 short, usually less than 0.4 times length of Htib (in 91% of measured specimens). Ex *P.terebinthus* (Southern Europe and North Africa) .... *G.utricularia* (Passerini) *sensu stricto*

– AS3 usually more than 0.4 times length of Htib (in 70% of measured specimens); sometimes shorter (down to 0.37 times) in alatae emerging from galls early (June–July). Ex *P.mutica* (South West and Central Asia) ...... *G.muticae* (Mordvilko)

7 AS4 usually more than 0.82 times length of HT2 (in 94% of measured specimens). AS6 (including PT) often longer than AS4 (in 70% of measured specimens). Ex *P.atlantica* (North Africa and Middle East) .... *G.rungsi* Hille Ris Lambers

– AS4 usually less than 0.82 times length of HT2, (in 80% of measured specimens) AS6 (including PT) usually shorter than AS4 (in 92% of measured specimens). Ex *P.palaestina* (Israel) .... *G.wertheimae* **sp.n.**

* The holocycle of *Geoica lucifuga* has not been described or confirmed experimentally, but Mordvilko (1935) suggested that the primary host might be *Pistacia sinensis*, and alatae (BL 2.1–2.2 mm) from galls on *P.sinensis* in Pakistan (leg. K. Naumann-Etienne) deposited first instars with chaetotaxy agreeing well with specimens of *G.lucifuga* from grass roots (G. Remaudière, pers. comm.). Very similar alatae (BL 1.6–1.9 mm) have also been collected from galls on *P.khinjuk* in Pakistan (BMNH, leg. M. Ghani). No information is available on gall morphology in either case.

Key to the alate sexuparae of the genus *Geoica*
(compiled by Dr V. F. Eastop)

1 Abdominal tergite VIII with numerous (60+) scattered attenuate hairs similar to those on anal plate ... *Geoica harpazi* **sp.n.**

– Abdominal tergite VIII with 7–20 usually spatulate hairs in a transverse row 2

2 Anal plate with numerous scattered hairs .... *Geoica utricularia* group

– Anal plate with 6–7 pairs of long stout hairs in a longitudinal double row in addition to a group of shorter hairs 3

3 Abdominal tergite V and VI bearing scattered hairs like abdominal tergite II–IV. Wax pores present only between abdominal tergites I–III except in very large specimens. Longest hair on marginal abdominal sclerite II–IV is 25–40 μm long .... *Geoica setulosa* (Passerini)

– Abdominal tergite V and VI with only a transverse row of hairs similar to those on abdominal tergite VII and VIII; Abdominal tergites II–IV with scattered hairs. Wax pores commonly present dorsally between abdominal tergites IV–VII as well as I–III. Longest hair on marginal abdominal sclerite II–IV is *c.* 60 μm long .... *Geoica lucifuga* (Zehntner)

Acknowledgments

We thank Dr Victor Eastop for permission to publish part of his manuscript key to Fordini sexuparae; Dr Georges Remaudière for the loan of specimens and for constructive comments; Dr G. Kh. Shaposhnikov for the loan of Mordvilko material; Professor Senator Vittorio Parisi for the loan of Passerini material; Ms Ora Manheim and Dr David Wool for helpful comments and the donation of specimens. We also thank Dr Richard Lane for constructive criticism of the manuscript and Ms Jenny Spence for help with statistical analysis.

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Accepted 4 January 1994