## Heather-feeding psyllids of the genus Strophingia (Homoptera)

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ABSTRACT. Multivariate analysis of morphological characters suggests that the genus Strophingia comprises eight distinct species, namely ericae (Curtis) [the type-species], australis sp.n., fallax Log., cinereae Hod., proxima sp.n., hispanica Hod. & Hollis, harteni sp.n., and arborea Log. Each species is fully characterized and an identification key is provided. A tentative phylogeny of the group is proposed. Among the newly described species, australis (host plant: Erica australis) occurs in Portugal, proxima (host plant: Erica arborea and possibly Calluna vulgaris) is found throughout the Iberian peninsula, while harteni (host plant: Erica azorica) is found on the Azores.

## Introduction

The genus Strophingia was erected by Enderlein (1914) to include a single representative, Psylla ericae Curtis, a species previously assigned to the genus Rhinocola by Förster (1848). Enderlein (1915) later dubiously referred a fossil insect, Strophingia oligocenica, to the genus. Subsequently several authors, including Ossiannilsson (1963) and Klimaszewski (1973, 1975), have regarded Strophingia as a synonym of Aphalaroida Crawford (1914), a genus otherwise restricted to fabaceous shrubs in the southern U.S.A. Other authors have stressed, correctly in my opinion, that Strophingia is a distinct palaearctic genus (Heslop-Harrison, 1952; Vondracek, 1957; Dobreanu & Manolache, 1962; Loginova, 1976).

Strophingia ericae remained the sole extant representative of the genus until Hodkinson (1971) described a further species, cinereae, from Britain and later recorded the same species from France (Hodkinson & White, 1979b). Recently Loginova (1976) described arborea and fallax from the Canary

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Islands and Madeira, and Hodkinson & Hollis (1980) described S. hispanica from Mallorca. I have now examined an abundance of additional material from the Azores, Portugal, Spain and France and a revision of the genus is now clearly required.

All the described Strophingia species are associated with host-plants within the genera Erica or Calluna (Ericaceae). The distribution of the genus appears to centre on the west Mediterranean region (Hodkinson, 1980) although S.ericae is known to occur throughout Europe and the European U.S.S.R., the range of its host plant Calluna vulgaris (Hodkinson, 1971).

Strophingia species are small, relatively immobile pysllids which seldom fly and it appears that within the genus there is a tendency to form isolated populations. For example, Hodkinson (1973a, b) demonstrated that in northern England ericae completed its life cycle in I year at low elevations whereas at high elevations it took 2 years. Subsequently Parkinson & Whittaker (1975) showed that the change-over from a 1 to a 2 year life cycle occurred abruptly along an altitudinal transect with continuous host plant cover. The upland 'race' had an inherently slower development rate than the lowland

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'race' and the two populations could be separated statistically using critical measurements of the Cu veins of the forewing. This tendency to form morphologically distinct populations is apparent in the material to hand. When set against the background that several of the described species are island forms, the taxonomy of the group becomes a fascinating dilemma in species interpretation. Multivariate statistical techniques have therefore been employed to identify major disjunctions and thereby help delineate species.

## Material examined

My initial philosophy was to ignore existing species groupings and conduct detailed objective analyses to test whether such groupings were justified. The names applied to material listed below result from these analyses. Material examined included all Strophingia specimens in the British Museum (Natural History) and my own personal collection together with type material of arborea and fallax deposited in the Zoological Museum, University of Helsinki. However, in ericae, a common species, specimens were selected to display maximum geographical and altitudinal variability. Full locality data for the new species are given in the later descriptions. The following abbreviated list gives the names of the countries/islands from which material was examined followed by the number of localities in parentheses: full locality data are available in mimeograph form from the author.

S.ericae: England (3), Scotland (1), France (1), Denmark (1), Norway (1), Portugal (3), Spain (1)

S. cinereae: England (1) (types), France (1), Corsica (1), Spain (1), Portugal (4)

S. hispanica: Spain, Mallorca (4) (types)

S. fallax: Madeira (2) (types)

S.arborea: Madeira (2), Tenerife (1) (types)

S. australis sp.nov.: Portugal (1) S. harteni sp.nov.: Azores (2)

S. proxima sp. nov.: Spain (5), Portugal (1)

## Strophingia Enderlein

Strophingia Enderlein, 1914: 233. Type-species: Psylla ericae Curtis, by monotypy.

Description. The following account complements Enderlein's meagre initial definition and serves to preclude repetitive description from the succeeding species diagnoses:

Small insects less than 2.5 mm in length. Head as broad as thorax, in lateral view globose, moderately deflexed; in dorsal view as Figs. 18 and 19; vertex flat or weakly convex, divided by median suture, rounded downwards anteriorly, with a smooth transition into the genae, the latter smoothly rounded and not markedly expanded; frons, which bears median ocellus apically, pyriform and borne on the underside of the head, barely visible in dorsal view; lateral ocelli very small, situated at outer posterior angles of vertex: clypeus globose, inconspicuous: labium relatively short, eyes hemispherical, pre-occipital lobes well developed. Antennae 10-segmented, at most three-quarters the width of head: basal 2 segments quadrate, remainder filiform, segment 3 the longest; single rhinaria placed at apices of segments 4, 6, 8 and 9; segment 10 with two apical setae. The shape of the head is relatively constant between species: Figs. 18 and 19 represent the extremes. Pronotum narrow, ribbon like, curved downwards anteriorly, transversely arched; propleurites long and narrow, divided by a curved vertical suture arising at mid-point of pronotum; parypterae and tegulae tubercular. Forewings short, at most 3 times head width, oval or rhomboidal, somewhat convex; membrane thick, translucent yellow with a transverse rugosity, venation as in Figs. 2-9; costal break present or absent; pterostigma present. Hindwings normally developed, thin membranous. Fore and mid legs simple: hind legs saltatorial, meracanthi well developed, apex of metatibia with a crown of six to eight (variable) thick black spines, basal metatarsus with two similar apical spines. Male proctiger simple, sometimes slightly lobed but without posterior processes (Figs. 10-17). Female terminalia (Figs. 38-50) normally developed, without characters of generic significance; circumanal pore ring with two complete rows of pores. All described species feed on Erica or Calluna (Ericaceae).

Diagnosis. Heslop-Harrison (1952) discusses in detail the separation of adult Strophingia from related genera including Aphala-

TABLE 1. Characters selected for principal components analysis. Measurements follow Hodkinson & White (1979a). Characters 35-39 are qualitative characters for use in later cladistic analysis and are derived from the quanti-

#### **OUANTITATIVE CHARACTERS**

### Size measurement

1. Head width

Ratio characters comparing relative size of major body parts

- 2. Antennal length : head width
- 3. Length of apical two segments of labium : head width
- 4. Forewing length: head width
- 5. Proctiger length (d or 9): head width

Ratio characters expressing wing shape and relative length of different veins

- 6. Forewing length : forewing breadth
- Length of vein Rs: forewing length
- 8. Length of vein Cu : forewing length
- 9. Distance from base of C + Sc to base of R<sub>S</sub>: forewing length
- 10. Length of vein M + M1+2: forewing length
- 11. Length of vein M1+2: M
- 12. Length of vein Cula : Culb
- 13. Distance from base of C+Sc to base of Rs: Rs
- 14. Length of vein Cu : Cu + M
- 15. Length of vein M1+2: M3+4

## Ratio characters expressing relative size and shape of terminalia

- 16. Length of d penis : proctiger
- 17. Length of d paramere : proctiger
- 18. Height of d sub-genital plate : proctiger
- 19. Length of ♀ circumanal pore ring: proctiger
- 20. Length of 9 ovipositor : proctiger

## QUALITATIVE CHARACTERS

- 21. Forewing rhomboidal (0), oval (1)
- 22. Costal break present (0), absent (1)
- 23. Forewing without maculation (0), with (1)
- 24. Vein Cula weakly arched (0), strongly arched (1)
- 25. Vein C+Sc not markedly bulged outwards (0), bulged (1)
- 26. Vein R<sub>S</sub> straight or curved away from costal margin (0), curved distally towards costal margin (1)
- 27. d paramere without posterior lobe (0), with (1)
- 28. d paramere with one apical denticle (0), with two apical denticles (1)
- 29. Apex of penis hooked (0), not hooked (1)
- 30. Apex of paramere broadly rounded (0), narrowly rounded (1)
- 31. 9 proctiger with shallow notch on dorsal margin (0), without notch (1)
- 32. 9 proctiger densely hairy, bearing long hairs (0), sparsely hairy (1)
- 33. 9 valvulae ventralis recurved apically (0), straight (1)
- 34. Apex of 9 sub-genital plate sharp (0), blunt (1)

## QUALITATIVE CHARACTERS DERIVED FROM NUMERICAL DATA FOR USE IN SUBSEQUENT CLADISTIC ANALYSIS

- 35. Forewing relatively narrow (0), broad (1)
- 36. Cell m<sub>1+2</sub> approximately equal to cell cu<sub>1</sub> (0), twice size (1)
- 37. Cell c + sc short (0), long (1)
- 38. Valvulae ventralis not curved away from ovipositor (0), curved away (1)
- 39. d paramere not bulged at basal anterior margin (0), bulged (1)

roida. While there is some convergence in adult characters between Strophingia and Aphalaroida, the respective nymphs are highly distinctive (I. M. White, personal communication).

# Character selection and principal components analysis

Characters selected for principal component analysis are given in Table 1. Qualitative characters which involved the use of subtle but apparent differences in the male genitalia were omitted at this stage as were certain quantitative characters, such as vertex length, which could not be reliably measured in slidemounted material. As Strophingia species are sexually dimorphic it was necessary to conduct separate analyses on males and females using the appropriate characters. All data sets were standardized to a mean of zero. In two specimens (australis) the antennae were missing and the antennal length:head width

ratio was adjusted to the mean of all specimens measured (i.e. to give it zero weighting). Principal component analysis was carried out on the character correlation matrices using an ICL statistical package implemented on the Liverpool Polytechnic computer.

Initial analyses were conducted using quantitative characters alone (characters 1-20). These were subsequently compared with analyses incorporating both quantitative and qualitative characters (1-34). The results from the different analyses were broadly similar but the effect of adding qualitative characters was to tighten the clusters and increase the percentage variance extracted. Therefore the following interpretations are based on analyses employing both character sets.

## Results of principal component anlyses

Fig. 1 illustrates the ordination of male and female specimens along principal component

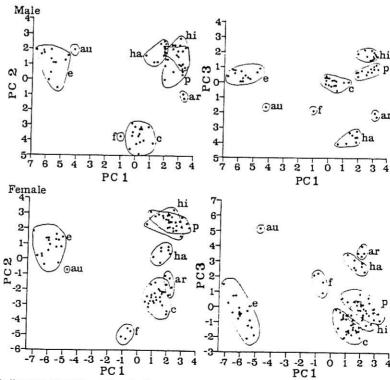


FIG. 1. Ordination of male and female Strophingia species along principal component axes 1-3. Each circle represents a specimen measured. Key: at = arborea, au = australis, c = cinereae, e = ericae, f = fallax, ha = harteni, hi = hispanica, p = proxima.

TABLE 2. Summary of variance extracted by principal component analysis and characters having highest weighting along components 1-5

	Variance extracted (%)										
PC	1		2		3		4		5		
<b>ರ</b>	39	9 59			69		76		81		
Q	38	38 59			70 74				78		
Charac	ters wit	h high	est load	lings							
PC rank order	1		2		3		4		5		
	đ	Q	ರ	Ò	đ	Q	d	Ŷ	<u> </u>	ç	
1	21	21	5	20	25	25	26	26	8	8	
2	29	23	18	33	30	4	14	25	3	3	
3	23	24	16	1	2	11	4	8	11	10	
4	24	31	17	34	28	22	3	7	5	19	
5	13	32	11	22	4	33	8	13	12	2	
5	9	5	27	11	1	26	6	6	25	1	
7	1	13	22	6	9	15	12	2	13	14	
				10 <del></del>				4	13	14	

axes 1-3. The variance extracted for each analysis and the characters having the highest loading along each axis are summarized in Table 2. In the males, eight groups separated out along these three axes and are considered to represent species. The two closest species, hispanica and proxima, separated further on axis 5. In the females the same groupings recurred except that hispanica and proxima overlapped on the first three axes but separated out on the fourth axis. Along this same axis arborea separated from proxima, hispanica and cinereae, and harteni was further distinguished from proxima.

The previously recognized species, ericae, cinereae, fallax, arborea and hispanica, were all demonstrated to be distinct and three new species, australis, proxima and harteni, were discriminated.

### Recognition of the species

Table 3 summarizes size measurements and the more important ratio characters of taxonomic significance for each species. This table should be used to confirm identifications made using the following key. In *cinereae* there is some geographic variation in the shape of the penis: this is illustrated in Figs. 30-33.

The penis of the unique male of fallax is damaged and is therefore not illustrated.

## Key to Strophingia species

- Costal break absent (Figs. 6-9). Male paramere (Figs. 24-27) without posterior lobe. Female proctiger (Figs. 46, 48, 50 and 52) shorter than head width. Male proctiger (Figs. 14-17) with slight posterior bulge. Larger species: head width d 0.50-0.67 mm, 9 0.60-0.76 mm. . . . . . . . .
- 2 Forewing (Fig. 2) broadly oval; round maculage present on membrane; vein Cu<sub>la</sub> strongly arched. Female proctiger (Fig. 38) sparsely hairy, without shallow notch in dorsal margin. Male paramere as Figs. 10 and 20, penis as Fig. 28.

ericae (Curtis)

- 3 Cell c + sc of forewing (Fig. 3) relatively long; vein R<sub>s</sub> curved apically towards costal margin;

TABLE 3. Size measurements (in mm), ranges for those ratio characters having a high weighting in principal components analysis, and known host plants of Strophingia spp.

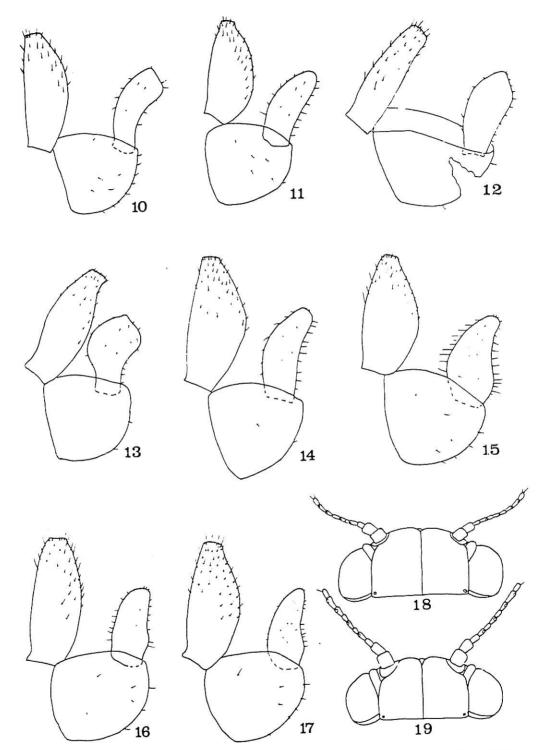
	ericae	australis	fallax	cinereae	proxima	hispanica	harte ni	arborea
Male								50 30000 1000 2000
Head width (HW)	0.48 - 0.55	0.47	0.47	0.50 - 0.54	0.57 - 0.63	0.63 - 0.67	0.55 - 0.59	0.50 - 0.60
Antennal length (AL)	0.32 - 0.41	-	0.36	0.29 - 0.34	0.32 - 0.37	0.32 - 0.34	0.37-0.40	0.30-0.37
Forewing length (FL)	0.99-1.10	1.07	1.19	1.08-1.24	1.28-1.46	1.39-1.50	1.25-1.41	1.30-1.47
Proctiger length (PL)	0.22 - 0.25	0.22	0.23	0.24 - 0.27	0.26 - 0.28	0.26-0.30	0.24- 0.27	0.24-0.26
Penis longth (P)	0.18 - 0.20	0.18	0.17	0.19 - 0.21	0.22 - 0.25	0.25 - 0.26	0.22 - 0.24	0.19 - 0.21
Paramere length (PA)	0.18-0.21	0.19	0.17	0.16-0.20	0.19-0.22	0.21 - 0.23	0.19-0.20	0.170.18
AL: HW	0.65 - 0.71	=	0.77	0.57 - 0.65	0.54 - 0.60	0.47 - 0.51	0.64 - 0.72	0.54 - 0.56
Ultimate two segs. labium : HW	0.37 - 0.42	0.46	0.39	0.34-0.38	0.32 - 0.35	0.37-0.39	0.34-0.39	0.38-0.39
FL:HW	1.94 - 2.16	2.30	2.57	2.11 - 2.32	2.13-2.38	2.14 - 2.31	2.16 - 2.46	2.36 - 2.47
FL: forewing breadth	1.89-2.09	2.16	2.27	2.08-2.35	2.13-2.32	2.09-2.21	2.10-2.24	2.22-2.26
Vein M.,,: M	0.41 - 0.89	0.51	0.87	0.81 - 1.41	0.60 - 0.95	0.30 - 0.72	0.58 - 0.89	0.59 - 0.60
Length C + Sc : FL	0.35 - 0.40	0.37	0.32	0.28 - 0.32	0.29 - 0.33	0.28 - 0.32	0.32 - 0.37	0.29 - 0.30
PL:HW	0.44 - 0.48	0.46	0.49	0.46 - 0.55	0.41 - 0.48	0.41 - 0.46	0.41 -0.45	0.43 - 0.44
P:PL	0.75 - 0.84	0.83	0.73	0.74 - 0.80	0.80 - 0.93	0.85 - 0.97	0.87 - 0.96	0.800.8
PA:PL	0.79 - 0.85	0.89	0.74	0.63 - 0.78	0.69 - 0.84	0.74 - 0.82	0.75 - 0.81	0.69 - 0.7

Female Head width (HW)	0.55-0.67	0.51	0.47-0.54	0.54-0.61	0.00	0.70-0.76	0.600.64	0.62-0.65
Antennal length (AL)	0.35-0.45	_	0.35 - 0.39	0.320.36	0.34-0.39	0.34-0.37	0.370.40	0.38-0.42
Forewing length	1.41-1.75	1.44	1.38-1.47	1.41-1.60	1.55-1.80	1.74-1.89	1.61-1.77	1.75-1.91
(FL) Proctiger length	0.57-0.67	0.59	0.53-0.58	0.47-0.55	0.49 - 0.54	0.54-0.61	0.55 0.58	0.50 0.56
(PL) Circumanal ring	0.13-0.17	0.13	0.14-0.15	0.13-0.16	0.13 - 0.17	0.14-0.16	0.16 - 0.18	0.16 - 0.18
length (CL) Ovipositor length	0.15-0.17	0,13	0.08-0.09	0.10-0.12	0.13-0.15	0.14 - 0.16	0,11-0.12	0.09 - 0.11
(OL) AL:HW	0.62-0.72		0.72-0.75	0.55-0.64	0.51-0.58	0.46-0.49	0.58-0.67	0.61-0.67
Ultimate two segs.	0.37-0.43	0.39	0.39 - 0.43	0.32 - 0.39	0.30-0.35	0.36-0.40	0.36-0.38	0.360.38
FL:HW	2.44-2.83	2.82	2.75 - 3.03	2.46 - 2.78	2.44-2.68	2.49-2.60	2.53-2.85	2.71-3.08
FL: forewing breadth	2.04-2.24	2.27	2.36-2.43	2.19-2.38	2.16-2.32	2.17-2.30	2,17-2.32	2.17-2.27
Vein M, : M	0.27-0.92	0.69	0.71 - 0.84	0.80 - 1.29	0.58 - 0.90	0.63 - 0.80	0.57 - 0.78	0.76 - 0.95
Length C + Sc : FL	0.31-0.36	0.35	0.28 - 0.31	0.26 - 0.31	0.25 - 0.32	0.25 - 0.33	0.28 - 0.31	0.27-0.30
PL:HW	1.01-1.15	1.16	1.06 - 1.12	0.83 - 0.96	0.75 - 0.82	0.77 - 0.84	0.86 - 0.94	0.80- 0.89
CA:PL	0.22-0.26	0.22	0.25 - 0.28	0.26 - 0.32	0.26 - 0.31	0.25 - 0.28	0.30-0.32	0.30-0.32
OL:PL	0.24-0.27	0.22	0.15 - 0.16	0.20 - 0.24	0.24 - 0.28	0.25 - 0.29	0.20 - 0.22	0.180.20
Host plants	Calluna vulgaris Erica cinerea?	Erica australis	Erica arborea	Erica cinerea E.arborea E.lucitanica	Erica arborea Calluna vulgaris?	Erica multiflora	Erica azorica	Erica arborea E.zucinulus

FIGS. 2-9. Strophingia & forewings. 2, ericae: 3, australis: 4, fallax: 5, cinereae: 6, proxima: 7, hispanica; 8, harteni; 9, arborea.

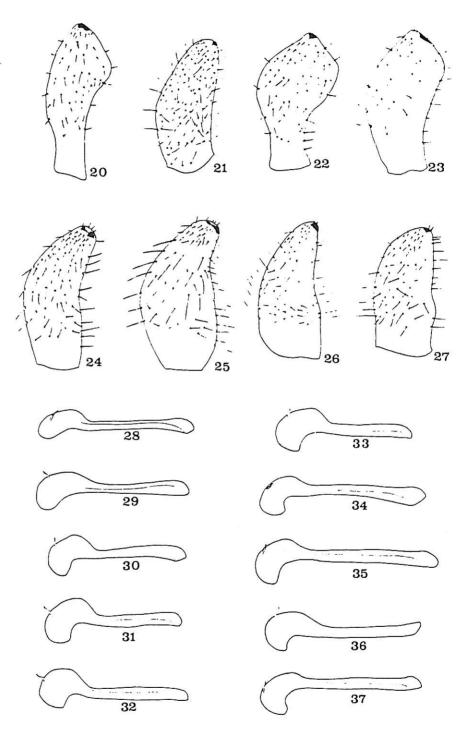
- 4 Forewing (Fig. 5) strongly rhomboidal, cell c + sc relatively broad in middle. Antennae shorter, at

Forewing (Fig. 4) less rhomboidal, tending to narrowly oval, cell c + sc narrower. Antennae longer, at least 0.71 times head width. Female terminalia (Fig. 42) longer, proctiger at least 1.06 times head width; ovipositor (Fig. 43) at most 0.16 times proctiger length. Male paramere (Figs. 12 and 23) with smaller posterior

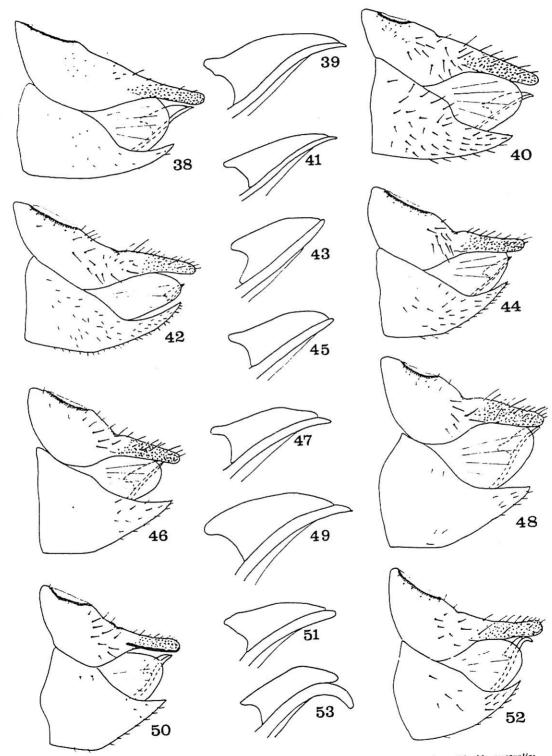


FIGS. 10-19. Strophingia & terminalia (lateral view) and heads (dorsal view). 10, ericae; 11, australis; 12, fallax (type, damaged); 13, cinereae; 14, proxima; 15, hispanica; 16, arborea; 17, harteni; 18, hispanica; 19, harteni.

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FIGS. 20-37. Strophingia of parameres (inner view) and apical portions of penis. 20, ericae; 21, australis; 22, cinereae; 23, fallax; 24, proxima; 25, hispanica; 26, harteni; 27, arborea; 28, ericae; 29, australis; 30, cinereae (England:type); 31, cinereae (Corsica); 32, cinereae (Portugal); 33, cinereae (France); 34, proxima; 35, hispanica; 36, harteni; 37, arborea.



FIGS. 38-50. Strophingia 9 terminalia (lateral view) and ovipositor. 38, 39, ericae; 40, 41, australis; 42, 43, fallax; 44, 45, cinereae; 46, 47, proxima; 48, 49, hispanica; 50, 51, harteni; 52, 53, arborea.

- 5 Male paramere (Figs. 14, 15, 24 and 25) drawn out into posteriorly curved, broad sub-parallel truncate apex which bears two denticles. Female ovipositor (Figs. 47 and 49) at least 0.24 times length of proctiger. Cell c + sc of forewing (Figs. 6 and 7) not markedly bulged outwards.
- 6 Male paramere (Fig. 25) with basal anterior margin bulged; penis as Fig. 35. Antennae less than 0.51 times head width. Distal two segments of labium greater than 0.36 times head width. Ratio of length of vein Cu<sub>2</sub>: forewing length less than 0.50 in d, 0.49 in ?. Larger species: head width d0.63-0.67 mm, 90.70-0.76 mm. Mallorca . . . . hispanica Hodkinson & Hollis
- Male paramere (Fig. 24) approximately parallel sided; penis as Fig. 34. Antennae more than 0.51 times head width. Distal two segments of labium less than 0.36 times head width. Cu<sub>2</sub>:forewing length greater than 0.50 in d, 0.49 in 9. Smaller species: head width d 0.57-0.63 mm, 9 0.63-0.70 mm. Iberian peninsula . . . . proxima sp.n.
- 7. Forewing (Fig. 9) with vein C + Sc strongly curved close to base, leading edge of wing almost straight in centre; cell c + sc shaped as in figure, strongly bulged. Paramere (Fig. 27) broadly acute at apex. Penis as Fig. 37. Ovipositor less than 0.20 times length of proctiger; valvulae ventralis (Fig. 53) strongly recurved at apex: subgenital plate (Fig. 52) with posterior apical projection sharp. Madeira and Canary Islands.

arborea Loginova

Forewing (Fig. 8) with vein C + Sc less strongly curved, leading edge of wing convex, cell c + sc less strongly bulged outwards. Paramere (Fig. 26) narrowly acute at apex. Penis as Fig. 36. Ovipositor greater than 0.20 times length of proctiger; valvulae ventralis (Fig. 51) less strongly recurved at apex: sub-genital plate (Fig. 50) blunt. Azores . . . . . . . . . . . . . harteni sp.n.

## Description of new species

As each new species conforms to the generic description, is fully illustrated and is separated from existing species both in the key and the later cladogram, there is no further need for discursive description. Type material as designated below is deposited in the British Museum (Natural History) unless otherwise stated.

Strophingia australis sp.n. (Figs. 3, 11, 21, 29, 40 and 41)

Holotype & PORTUGAL: S. Braz, ~ 300 m, 30.iv.1978 from Erica australis (Bink-Moenen).

Paratype. 1 9, data as holotype.

Strophingia proxima sp.n. (Figs. 6, 14, 24, 34, 46 and 47)

Holotype &, SPAIN: Gerona, 3-9 km La Bisbal - Calonge Rd, 1.vi.1975 (Hollis).

Paratypes. 8 d, 6 9, data as holotype; 2 d, 2 9, SPAIN: Gerona, Llafranch, 2.vi.1975 (Hollis); 1 d, 4 9, SPAIN: Huelva, 20 km S. Almante, 13.vi.1977, from Erica arborea (Hollis). 2 9, labelled 'Andalusia, Rambur collection, ericae Curt. M. Leth'. 4 9, labelled 'Andalusia, Rambur collection, sp.n.'. 4 d, 18 9, PORTUGAL: nr. Nazare, 17.ix.1979, on Erica sp. (Lienhard) (in coll. D. Burckhardt).

Strophingia harteni sp.n. (Figs. 8, 17, 19, 26, 36, 50 and 51)

Holotype &, AZORES: Flores, 24.ix.1979, from E.azorica (van Harten).

Paratypes. 8 &, 19 \, data as holotype. 1 \, labelled 'Azores: S. Miguel, Furnas, 23.vii—1.vii. Frey. Rhinocola'.

## Cladistic relationships with the genus Strophingia

Fig. 54 is the most parsimonious cladistic estimate of phylogeny within the genus based on an analysis of the qualitative characters 21-34 and on a further series of qualitative characters (35-39) derived from the initial quantitative character set (Table 1). In each case the (0) state is assumed to be the plesiomorphic state and the (1) state the apomorphic. All characters are used in the cladogram; with the exception of numbers 21, 27 and 34, each is uniquely derived. In consequence, in the most parsimonious solution, characters 21, 27 and 34 must be regarded as being multiply derived. Strophingia proxima, hispanica, harteni and arborea form

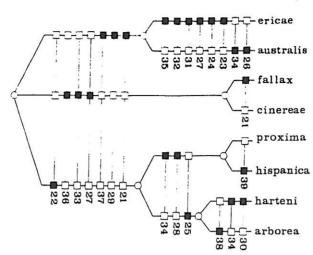


FIG. 54. Cladogram to illustrate proposed phylogeny of *Strophingia* species. Black squares are apomorphic character states, open squares are plesiomorphic character states. Numbers refer to characters listed in Table 1. The ancestral species is assumed to have possessed all characters in the plesiomorphic state. Characters 21, 27 and 34 are shown as being multiply derived.

a single clade defined by the absence of a costal break: fallax/cinereae and ericae/australis form two further separate clades. There are no derived characters which define the exact branching sequence between these three major clades and they are drawn as arising from a trifurcation. However, the evidence suggests that the fallax/cinereae clade is closer to the ericae/australis clade than to the proxima/ arborea clade. For instance, ericae, fallax and cinereae share the same unique general paramere shape and ericae, australis and fallax all possess similar elongate female terminalia. Furthermore, all these species have retained the costal break. This suggests that perhaps the ericae/australis and the fallax/cinereae clades should split subsequent to the separation of the proxima group.

The possible isolating mechanisms which led to speciation are apparent in both the fallax and proxima groups. In the former, fallax occurs on Madeira whereas cinereae is confined to mainland Europe, Britain and Corsica. In the latter group, proxima is found on the Iberian peninsula, while the remainder are found on isolated islands: hispanica occurs on Mallorca, harteni on the Azores and arborea on Madeira and the Canaries. The mechanism leading to the separation of ericae and australis is less obvious: ericae is distri-

buted throughout Europe, whereas australis is known only from Portugal.

The extent to which host-plant isolation in both a taxonomic and a geographical sense has contributed to speciation within the genus remains unclear as the host plant ranges of the different species are yet to be fully defined.

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