

SYSTEMATIC STUDIES ON MITES OF THE SUPERFAMILY EUPODOIDEA
(ACARI: ACARIFORMES) BASED ON THE FAUNA OF THE BRITISH ISLES

Volume 1

by

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1. ABSTRACT

Aspects of the systematics of the Eupodoidea, a poorly known superfamily of predominantly soil- and litter-dwelling mites, are studied.

The literature concerning the superfamily is surveyed and past and present systematic positions are reviewed.

Using material collected in the British Isles, a detailed account of external morphology is given. Many structures are illustrated by scanning electron micrographs, some for the first time.

Both phenetic and cladistic methods of analyses are used to investigate the validity of supra-specific taxa. The species included in the analyses comprise those found in the British fauna plus type species, where possible, and representative examples of genera not found in the British Isles. The resulting classifications are described and the merits of the two methods considered.

A revised supra-specific classification is proposed in which the species are classified into four families. Four new genera are proposed, while 17 genera and subgenera are considered to be invalid. One of the new taxa, *Caleupodes reticulatus*, shows external evidence of opisthosomal segmentation, a feature which is used to interpret the relationship of segments with associated setae and lyrifissures

The 40 species of eupodoid found in the British fauna are diagnosed, described and illustrated. Ten of these are new to science while 19 are new British records. Three new synonymies and 10 new combinations are proposed, three species are returned to their original genus, while a new type species for the genus *Eupodes* is designated and the date of establishment of two others is clarified. Identification keys are provided to the families and genera of the world and to the species of the British Isles.

Examination of the active life stages of five species enabled certain ontogenetic trends in segmental and setal addition to be recorded.

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CONTENTS

VOLUME 1

	Page
1. ABSTRACT	2
2. ACKNOWLEDGEMENTS	3
3. LIST OF TABLES	8
4. LIST OF FIGURES	9
5. INTRODUCTION	14
6. A REVIEW OF THE CLASSIFICATION OF THE SUPERFAMILY EUPODOIDEA BANKS 1894	17
6.1 Historical survey of the changes in definition and composition of the superfamily Eupodoidea	17
6.2 Review of the classification of taxa currently included in the Eupodoidea	27
6.3 Current systematic position of the Eupodoidea	37
7. STUDY OF THE EXTERNAL MORPHOLOGY OF THE EUPODOIDEA	44
7.1 Material examined	44
7.2 Methods	47
7.2.1 Collection of specimens	47
7.2.2 Extraction of specimens from habitat samples	54
7.2.3 Preparation of specimens for light microscopy	61
7.2.4 Preparation of specimens for scanning electron microscopy	63
7.3 Description of external morphology of the Eupodoidea	64
7.3.1 Terminology	64
7.3.2 General appearance	69
7.3.3 Divisions of the body	69
7.3.4 The integument and associated structures	70

	Page
7.3 Description of external morphology (cont.)	
7.3.5 Gnathosoma	75
7.3.6 Idiosoma - dorsum	80
7.3.7 Idiosoma - venter	83
7.3.8 Legs	86
7.3.9 Immature stages	90
8. SYSTEMATIC ANALYSIS AND CLASSIFICATION	127
8.1 Introduction	127
8.2 Phenetic analysis	130
8.2.1 Principal co-ordinates analysis of the Eupodoidea	131
8.2.2 The data matrix	136
8.2.3 Interpretation of the results	147
8.2.4 Runs of the analyses	149
8.2.5 Survey	180
8.3 Cladistic analysis	182
8.3.1 Cladistic analysis of the Eupodoidea	189
8.3.2 Results of the analysis	196
8.3.3 Survey	213
8.4 A discussion of systematic methods and their application to the Eupodoidea	214
9. A PROPOSED REVISION OF THE SUPRA-SPECIFIC CLASSIFICATION OF THE SUPERFAMILY EUPODOIDEA	228
9.1 Familial classification	228
9.2 Generic classification	230
9.3 Taxonomic summary	238

	<u>Volume 2</u>	Page
10. DESCRIPTION OF THE TAXA		241
10.1 Superfamily Eupodoidea Banks		245
10.1.1 Family Eupodidae Koch		250
10.1.1.1 <i>Eupodes</i> Koch		255
10.1.1.2 <i>Alloeupodes</i> n. gen.		285
10.1.1.3 <i>Aneboeupodes</i> n. gen.		295
10.1.1.4 <i>Benoinyssus</i> Fain		311
10.1.1.5 <i>Caleupodes</i> n. gen.		335
10.1.1.6 <i>Claveupodes</i> Strandtmann & Prasse		344
10.1.1.7 <i>Cocceupodes</i> Thor		367
10.1.1.8 <i>Linopodes</i> Koch		421
10.1.1.9 <i>Subeupodes</i> n. gen.		435
10.1.2 Family Penthaleidae Oudemans		445
10.1.2.1 <i>Penthaleus</i> Koch		448
10.1.3 Family Penthalodidae Thor		461
10.1.3.1 <i>Penthalodes</i> Murray		464
10.1.4 Family Rhagidiidae Oudemans		479
10.1.4.1 <i>Rhagidia</i> Thorell		483
10.1.4.2 <i>Coccorhagidia</i> Thor		521
10.1.4.3 <i>Latoempodia</i> Zacharda		560
10.1.4.4 <i>Shibaia</i> Zacharda		568
11. ONTOGENETIC DEVELOPMENT		577
11.1 Introduction		577
11.2 Species studied		578
11.3 Ontogeny of the Eupodoidea		579
11.4 Remarks		589
12. SUMMARY		591

13. REFERENCES	596
14. APPENDICES:	
I. Run 1 of phenetic analysis - nearest neighbours list	614
II. Run 2 of phenetic analysis - nearest neighbours list	619
III. Run 3 of phenetic analysis - nearest neighbours list	622
IV. Baker, A S (1985)	

3. LIST OF TABLES.

1. Composition of the superfamily Eupodoidea from establishment to the modern concept.
2. Survey of systematic positions accorded to taxa of the superfamily Eupodoidea.
3. The systematic position of the Eupodoidea in recent classifications.
4. Comparison of terms used by various authors for the external morphology of eupodoid mites.
5. Characters and character states used in phenetic analyses.
6. Operational Taxonomic Units used in taxonomic analyses.
7. Character polarizations used in cladistic analysis.
8. Comparison of supra-specific classifications resulting from phenetic and cladistic analyses.
9. A revised supra-specific classification proposed for the superfamily Eupodoidea.
10. The eupodoid fauna of the British Isles.

4. LIST OF FIGURES

(Main titles only are given)

1. British Isles: principal collection sites.
2. Adapted 'UniVac' portable suction sampler.
3. 'UniVac' portable suction sampler in operation.
4. Apparatus for the extraction of specimens from habitat samples.
5. Details of extraction apparatus.
6. Illustration of positional terms.
7. External morphology of the Eupodoidea.
8. Setiform structures.
9. External morphology, gnathosoma and lyrifissures.
10. External morphology, palps and epivertex.
11. External morphology, genital area.
12. Tarsal chaetotaxy: posterolateral aspect of generalized eupodid tarsus I.
13. Life stages - distinguishing features in genital and anal regions.
14. Ornamentation of the integument.
15. Prodorsum and gnathosoma.
16. Setal ornamentation.
17. Aspects of the integument and setiform structures.
18. Rhagidial organs and famuli.
19. Solenidia.
20. Prodorsal trichobothria and bothridia.
21. Lyrifissures.

22. Gnathosoma.
23. Chelicerae, palps and supracoxal setae.
24. Anus and genitalia.
25. Anal region.
26. Leg articulations and subdivision, *Eupodes alaskanensis*.
27. Apotela.
28. Claparède organs and genital papilla.
29. Immature stages.
30. Principal co-ordinates of the 70 OTUs included in Run 1 of the phenetic analysis.
31. Single-linkage cluster analysis of the 70 OTUs included in Run 1 of the phenetic analysis.
32. Single-linkage cluster analysis of the 40 OTUs included in Run 2 of the phenetic analysis. Dotted line indicates generic phenon.
33. Minimum spanning tree for the 40 OTUs included in Run 2 of the phenetic analysis.
34. Adapted similarity matrix for the 40 OTUs included in Run 2 of the phenetic analysis.
35. Principal co-ordinates for the 40 OTUs included in Run 2 of the phenetic analysis.
36. Single-linkage cluster analysis of the 40 OTUs included in Run 2 of the phenetic analysis. Dotted lines indicate alternative familial phenons.
37. Principal co-ordinates of the 35 OTUs included in Run 3 of the phenetic analysis.
38. Single-linkage cluster analysis of the 35 OTUs included in Run 3 of the phenetic analysis.

39. Minimum spanning tree of the 35 OTUs included in Run 3 of the phenetic analysis.
40. Adapted similarity matrix of the 35 OTUs included in Run 3 of the phenetic analysis.
41. Methods of out-group comparison.
42. Cladogram showing the initial division of the superfamily Eupodoidea.
43. Cladogram of the family Rhagidiidae.
44. Cladogram of the family Penthaleidae.
45. Cladogram of the family Penthaleodidae.
46. Cladogram of the family Eupodidae.
47. Demonstration of measurement of body and appendages.
- 48 & 49. *Eupodes abbreviatus* n.sp.
- 50 & 51. *Eupodes alaskanensis*.
- 52 & 53. *Eupodes striatus* n.sp.
- 54 & 55. *Eupodes truncatus* n.sp.
- 56 & 57. *Alloeupodes interruptus* n.sp.
- 58 & 59. *Aneboeupodes minimus* n.sp.
- 60 & 61. *Aneboeupodes magnus* n.sp.
- 62 & 63. *Benoinyssus najae*.
- 64 & 65. *Benoinyssus ereynetoides*.
- 66 & 67. *Benoinyssus momeni*.
- 68 & 69. *Caleupodes reticulatus* n.sp.
- 70 & 71. *Claveupodes delicatus*.
- 72 & 73. *Claveupodes juvenalis* n.sp.
- 74 & 75. *Claveupodes ornatus* n.sp.
- 76 & 77. *Cocceupodes australis*.

- 78 & 79. *Cocceupodes breweri*.
80 & 81. *Cocceupodes minutus* n.sp.
82 & 83. *Cocceupodes paradoxus*.
84 & 85. *Cocceupodes setosus*.
86 & 87. *Cocceupodes stellatus*.
88 & 89. *Cocceupodes trisetatus*.
90 & 91. *Linopodes agitatorius*.
92 & 93. *Linopodes motatorius*.
94 & 95. *Subeupodes boernerii*.
96 & 97. *Penthaleus longipilis*.
98 & 99. *Penthaleus minor*.
100 & 101. *Penthalodes ovalis*.
102 & 103. *Penthalodes nitidus*.
104 & 105. *Rhagidia arena*.
106 & 107. *Rhagidia clavicrinata*.
108 & 109. *Rhagidia montana*.
110 & 111. *Rhagidia punkva*.
112 & 113. *Rhagidia spelaea*.
114 & 115. *Coccorhagidia clavifrons*.
116 & 117. *Coccorhagidia evansi*.
118 & 119. *Coccorhagidia macrostella*.
120 & 121. *Coccorhagidia pittardi*.
122 & 123. *Coccorhagidia subterranea*.
124 & 125. *Latoempodia macroempodiata*.
126 & 127. *Shibaia heteropoda*.

128. *Caleuodes reticulatus*: illustrating the application of Grandjean's (1947) notation system for opisthosomal segments, setae and lyrifissures.
129. Ontogenetic development: Posterior view of larvae (L) and protonymphs (P) illustrating the three schemes of segmental and setal addition.
130. *Penthaleus minor*, dorsum of larva.
131. Ontogenetic development: illustrating setal addition in the podosomal and genital areas.

5. INTRODUCTION

Mites of the superfamily Eupodoidea are small to medium in size (175 to 2000 μ m long), weakly sclerotized and, in life, often colourful and active. The superfamily is classified in the diverse suborder Actinedida (= Prostigmata, in part) which, together with the suborders Acaridida and Oribatida, constitute the order Acariformes.

Eupodoids have a wide geographical range, representatives having been found in most areas of the world, including both polar regions. Although the greatest numbers of species have been described from Japan, Malaysia, Antarctica and north-west and eastern Europe, this reflects the areas which have received most attention from collectors. A number of species are apparently cosmopolitan, but the many gaps in distribution records mean that definitive geographic ranges are not known.

Eupodoid mites are all terrestrial and have exploited a wide range of habitats where moist conditions prevail. The greatest number, in terms of both species and individuals, are to be found in the top few centimetres of grass- and woodland soils. Many occur in habitats such as moss, decomposing wood and on fungi. Others have colonized coastal, cavernicolous and montane habitats, while one species has even been collected from steam vents in Hawaii.

The superfamily includes both phytophagous and predatory species. Although there is little detailed knowledge of food preferences, the majority of species are considered to be phytophages, feeding mainly on lower plants such as algae, fungi and lichens. The large numbers that occur in the soil play a part as secondary decomposers of plant debris. In addition, four species are considered to be economically important

pests of horticultural and agricultural plants in certain parts of the world. The food of predatory species includes nematodes, Collembola, small mites and the eggs of these animals.

Despite their ubiquity, eupodoids are easily overlooked due to their small size and retiring habits. Furthermore, they readily succumb to desiccation and are easily lost if habitat samples dry too quickly during Berlese funnel extractions. In alcohol, the colour is leached out of these mites leaving them translucently white and inconspicuous.

The Eupodoidea comprises 487 nominate species, many of which cannot be identified on the basis of their inadequate original descriptions and nor can they be checked as type material is often unavailable through loss, destruction or lack of designation. Several classifications have been proposed and the species are, at present, grouped into between 11 and 32 genera which in turn belong to between three and five families. The uncertainty of specific identities and the disparity between the numbers of both families and genera reflect the lack of detailed knowledge of external morphology and the differing opinions of authors on the significance of certain structures.

The principal works on the superfamily are by Thor and Willmann (1941), a series of papers by Shiba (1969-1976) and by Strandtmann (1963-1981) and a revision of one of the families by Zacharda (1980). The most useful keys appear in the works of Strandtmann (1970, 1971, Strandtmann & Prasse 1976). These allow preliminary identification to family and, in most cases, to genus but they have inevitably become out-of-date as new taxa have been discovered.

Eupodoids are abundantly represented in the British fauna. They are frequently collected during the course of ecological investigations and faunistic studies (for example, Hull 1918, 1930, Halbert 1915, 1920, Evans

1952, 1954, Luxton 1967, Turk 1967, 1972, Wood 1967, 1967a & b, Purvis 1982) but, since many of the species names given are not adequately defined for reliable determination, the true identity of some of this material remains uncertain. Twenty species of eupodoids are included in the most recent comprehensive check-list of British mites (Turk 1953), while seven have since been added by other workers. The British fauna is, therefore, represented in the literature by 27 species classified in nine genera.

As a result of the uncertainty in the classification of the Eupodoidea, it was decided to study the taxonomy of the poorly documented, but readily available, British fauna. Such a study inevitably involves the examination of taxa from other geographical regions and, as many of the taxa are apparently cosmopolitan, the results would have implications for the world-wide eupodoid fauna. The objectives of this study can, therefore, be outlined as follows:

1. To collect British eupodoid mites.
2. To survey eupodoid external morphology in order to clearly interpret previously observed characters and to identify new ones with the aid of scanning electron and phase contrast microscopy.
3. To investigate the validity of supra-specific rankings using phenetic and cladistic methods of analysis.
4. To diagnose, describe and provide identification keys to the British fauna.
5. To examine immature stages in order to observe trends in ontogenetic development and to identify the homologues of structures present in other taxa.

6. A REVIEW OF THE CLASSIFICATION OF THE SUPERFAMILY

EUPODOIDEA BANKS 1894

This section deals with the changes that have occurred in the concept of the superfamily and presents a historical review of the classification.

The review is divided into three parts. The first (section 6.1), describes the characters used by authors in defining the superfamily and the taxa which they included as a consequence. Secondly (section 6.2), an account is given of the various systematic positions of taxa now recognized to be eupodoid before the erection of the superfamily. Also included in this part are the positions occupied by eupodoids in classifications where authors do not use the rank of superfamily. Lastly (section 6.3), the current systematic position of the Eupodoidea is examined.

6.1 HISTORICAL SURVEY OF THE CHANGES IN DEFINITION AND COMPOSITION OF THE SUPERFAMILY EUPODOIDEA

The composition and definition of the superfamily Eupodoidea has been considerably modified since it was originally proposed by Banks in 1894¹. Early definitions place emphasis on the position of the stigmata and the form of the palp to separate taxa, whereas the modern concept of

¹ Wainshtein (1978) erroneously attributes the authorship of the superfamily to Koch (1842). In this work, however, Koch describes the family Eupodidae only.

the Eupodoidea essentially developed from the discovery of recumbent solenidia, rhagidial organs, on certain leg segments and the use of their presence to unite the taxa bearing them. The various compositions of the superfamily Eupodoidea are given in Table 1. In the following account, details will only be given of the components of families now classified in the superfamily Eupodoidea, the members of other families can be obtained from Table 1.

Banks first described the Eupodoidea in his report on the mites of the United States of America (Banks 1894) as one of the eight superfamilies into which he divided the fauna. There was no text description of the superfamilies; their diagnostic characters being given in an identification key. He distinguished between them on the basis of the appendages and the presence of eyes and sclerotized dorsal plates. Eupodoid mites were defined by the following character states:

- 1) Not living in galls or in flesh, adults with eight legs.
- 2) Land mites.
- 3) Stigmata present (tracheate), no chitinous rods visible.
- 4) Last joint of palpus simple.
- 5) Stigmata not above on the cephalothorax and without seta, body usually partly soft.
- 6) Mandibles not forming a serrate proboscis, smaller species.
- 7) Stigmata at base of mandibles, body wholly soft, no sucker at tip of legs, eyes often present.'

According to Banks, this definition of eupodoid mites embraced three families, but he only dealt with the two he had observed in the U.S.A. and did not even name the third. These two families, the Bdellidae Dugès (now classified in the superfamily Bdelloidea Dubinin) and the Eupodidae Koch, were separated respectively by possessing three or either five or

Table 1. Composition of the superfamily Eupodoidea from establishment to the modern concept.

BANKS (1894)	BANKS (1904)	EWING (1910)	BANKS (1915)	LOMBARDINI (1938)	THOR & WILLMANN (1941)	CUMLIFFE (1955)	
(families & genera)	(families & genera)	(families)	(families, subfamilies & genera)	(families)	(families & genera)	(families)	
Eupodidae	Eupodidae	Eupodidae	Eupodidae	Eupodidae	Eupodidae	Nicoletiellidae	Eupodidae
<i>Eupodes</i>	<i>Eupodes</i>		Eupodinae		<i>Eupodes</i>	<i>Labidostomna</i>	
<i>Linopodes</i>	<i>Linopodes</i>		<i>Eupodes</i>		<i>Cocceupodes</i>	<i>Eunicolina</i>	
<i>Rhagidia</i>	<i>Notophallus</i>		<i>Notophallus</i>		<i>Linopodes</i>	<i>Nicoletiella</i>	
	<i>Rhagidia</i>		<i>Penthaleus</i>	Bdellidae	<i>Prottereunetes</i>		
	<i>Tydeus</i>		<i>Rhagidia</i>		Penthalodidae	Tydeidae	Penthalodidae
			<i>Ereynetes</i>		<i>Penthalodes</i>	<i>Tydeus</i>	
			<i>Tydeus</i>		<i>Chromotydaeus</i>	<i>Triophytydeus</i>	
			Alichinae		<i>Stereotydeus</i>	<i>Brachytydeus</i>	
			<i>Alichus</i>		<i>Tectopenthalodes</i>	<i>Microtydeus</i>	
			<i>Biwichaëlia</i>			<i>Coccotydeus</i>	
Bdellidae	Bdellidae	Bdellidae	Bdellidae	Cryptognathidae	Penthaleidae	<i>Tydaëolus</i>	Rhagidiidae
<i>Bdella</i>	<i>Bdella</i>		<i>Bdella</i>		<i>Penthaleus</i>	<i>Scolotydaeus</i>	
<i>Eupalus</i>	<i>Cyta</i>		<i>Cunaxa</i>		<i>Halotydeus</i>	<i>Pronematus</i>	
<i>Scirus</i>	<i>Eupalus</i>		<i>Cyta</i>			<i>Proctotydaeus</i>	
	<i>Scirus</i>		<i>Eupalus</i>			<i>Lasiotydaeus</i>	
			<i>Scirula</i>			<i>Melanotydaeus</i>	
			<i>Scirus</i>	Cunaxidae	Rhagidiidae	<i>Retetydeus</i>	
			Cryptognathidae		<i>Rhagidia</i>	<i>Coleotydeus</i>	
			<i>Cryptognathus</i>		<i>Poecilophysis</i>	<i>Lorryia</i>	
					<i>Coccorhagidia</i>		
				Labidostomidae	Cryptognathidae	Pachygnathidae	
					<i>Cryptognathus</i>	<i>Pachygnathus</i>	
						<i>Biwichaëlia</i>	
					Ereynetidae	<i>Nanorchestes</i>	
					<i>Riccardoella</i>	<i>Gainia</i>	
					<i>Ereynetes</i>	<i>Sebaia</i>	
					<i>Upsereynetes</i>	<i>Caenonychus</i>	
						<i>Sphaerolichus</i>	
					Bdellidae	<i>Hybolicus</i>	
					<i>Bdella</i>	<i>Leptalicus</i>	
					<i>Spinibdella</i>	<i>Alicorhagia</i>	
					<i>Trachymolgus</i>	<i>Speleorchestes</i>	
					<i>Scirus</i>	<i>Coccorchestes</i>	
					<i>Biscirus</i>		
					<i>Molgus</i>		

four palpal segments. Three genera were included in the family Eupodidae: *Eupodes* Koch, *Linopodes* Koch and *Rhagidia* Thorell. In notes elsewhere in this work (p. 213), Banks also showed that he considered *Notophallus* (later to be synonymized with *Penthaleus* Koch) to belong to the Eupodidae. However he also stated (on p. 221) that a recorded species of *Penthaleus* from Florida was not a eupodid, but he did not indicate to which superfamily it should belong.

In Banks' later studies (1904, 1915), which revised and extended his work of 1894, European taxa were also considered. The Acari were again divided into eight superfamilies but the characters used to differentiate them were somewhat amended, taking more account of body and palpal form. The Eupodoidea consequently were defined by the following character states:

- '1) Abdomen not annulate nor prolonged behind; always with eight legs.
- 2) No distinct spiracle in a stigmal plate on each side of the body (usually below) above the third or fourth coxae or a little behind.
- 3) Body soft, without a specialized seta arising from pore near each posterior corner of the cephalothorax.
- 4) Not living in water.
- 5) Palpi usually of 4 or 5 joints, free; rarely with ventral suckers near genital or anal openings; eyes often present; tarsi never end in suckers; body usually divided into cephalothorax & abdomen; rod-like epimera rarely visible; adults rarely parasitic.
- 6) Last joint of palpi never forms a 'thumb' to the preceding joint; palpi simple, or rarely formed to hold prey; body but with few hairs.'

In his study of 1904, Banks again stated that there were three eupodoid families but named only two. The Bdellidae and Eupodidae were here distinguished from each other by the form of the chelicerae, the prodorsal setation, the length of tarsus I relative to tibia I and the presence of eyes. Eupodids were therefore defined as mites with 'Palpi never geniculate, not fitted for grasping prey; beak small; cephalothorax with bristles in different arrangement; last joint of leg I shorter or but little longer than preceding joint; eyes when present, near posterior border'. It is interesting to note that figures of *Linopodes antennaepes* Banks and *Rhagidia pallida* given in this paper showed a character now used in the modern definition of the superfamily, namely the naso protruding from the anterior of the prodorsum. The text, though, makes no mention of this feature. The Eupodidae was regarded as being made up of the genera *Eupodes*, *Linopodes*, *Notophallus*, *Rhagidia* and *Tydeus* Koch (the latter genus is now classified in the family Tydeidae, superfamily Tydeoidea). In his account of the Eupodidae, Banks (1904) also suggested that *Erynetes* (*lapsus pro Ereynetes* Berlese) and *Penthaleus* were also eupodoid genera. Here, he also referred, for no obvious reason, to the genus *Alycus* (*lapsus pro Alychus* Koch, now classified in the family Pachygnathidae) but considered it to belong to another, non-specified, family. In this account of the Acari, the key characters of the superfamilies and families were unchanged but the family Cryptognathidae was included in the Eupodoidea. As this family was not described by Oudemans until 1902, it is not clear whether Banks regarded it as the unspecified third eupodoid family mentioned in 1894 and 1904.

Subsequently, Banks (1915) divided the Eupodidae into two subfamilies. The Alichinae, including the genus *Alychus*, were

distinguished from the Eupodinae by possessing three pairs of genital suckers (=genital papillae), submedian propodosomal (=prodorsal) sensory setae and a more or less distinctly segmented opisthosoma. The Eupodinae were defined by the possession of two pairs of genital suckers, the lack of submedian propodosomal sensory setae and the indistinctly segmented opisthosoma. Banks stated that the Eupodinae contained many genera but only listed the following which he considered to be the principal ones: *Ereynetes*, *Eupodes*, *Linopodes*, *Notophallus*, *Penthaleus*, *Rhagidia* and *Tydeus*. The same figures of *Linopodes antennaepes* and *Rhagidia pallida* that appeared in Banks (1904) were used in this work but, again, there was no description of the naso.

In the meantime, Ewing (1910) had classified the Eupodoidea using similar characters to Banks. Eupodoids were placed in the suborder Robustiformia, comprising mites with a short, compact body without an annulated opisthosoma, and then into the tribe Prostigmata by virtue of being terrestrial forms with tracheae opening near the base of the chelicerae. The key characters of the Eupodoidea were the palp tibiotarsus never forming a thumb and legs without swollen tarsi. Again, the families Bdellidae and Eupodidae made up the superfamily, separated from each other by the form of the palps and the setation of the prodorsum, with additional comments on leg length and mobility of the Eupodidae. Hence, the key characters of eupodid mites were 'Palpi not raptorial or geniculate. Legs often very long. Acarina with very agile movements, often sideways or backwards.' Member genera of the families were not listed.

The year 1915 also saw the first published observations of rhagidial organs. In his description of *Rhagidia mordax*, Oudemans (1915) remarked on two oblique grooves on tarsus II, each with a recumbent seta lying in

it. Thor (1934a) observed these organs in other species of *Rhagidia* and, at the same time, proposed the term '*Rhagidia*-organ'. Thor (1934c) also observed structures on tarsi I and II of *Penthaleus major* Dugès which he thought similar to rhagidial organs, though sufficiently different to warrant giving them their own name of '*Penthaleus*-organ'. With the recognition of the variation in this type of solenidion, however, this term has not persisted. The number of genera with species seen to possess rhagidial organs was further increased by Haarløv (1942) who observed them in *Eupodes variegatus* Koch, *E. viridis* Oudemans and in *Cocceupodes clavifrons* (Canestrini). Having discovered they occurred in genera other than *Rhagidia*, Haarløv also considered it apt to rename these structures 'Sig Thor organs', after the Norwegian acarologist, but the proposed change has never been widely accepted.

Other early workers also based their classifications of mites on similar characters to Banks and without reference to the rhagidial organs. The Eupodoidea was one of four superfamilies Lombardini (1938) classified in the suborder Prostigmata. Again, the lack of an opposable palptarsus singled out eupodoid mites. The families Cunaxidae Thor and Labidostommidae Oudemans (now respectively classified in the superfamilies Bdelloidea and Labidostommatoidea) were added to the three listed by Banks (1915).

In the extensive work of Thor and Willmann (1941), the Eupodoidea (erroneously cited as being described in 1904) is given subordinal status and the complement of genera vastly increased. Here, eupodoids are regarded as those mites with chelate chelicerae and with relatively simple, three to five segmented palps supporting simple setae, a definition that embraced the following 10 families: Tydeidae, Ereyneidae, Eupodidae, Penthaleidae, Penthaleidae, Rhagidiidae,

Nicoletiellidae, Cryptognathidae, Pachygnathidae and Bdellidae. It is interesting to note that, in this work, Thor and Willmann give the possession of rhagidial organs as a familial character of the Rhagidiidae, yet they used figures showing the palp tibiotarsal rhagidial organ in eupodid species, for example, *Eupodes fusifer* Canestrini and *Linopodes motatorius* (L.). No reference, however, is made to this organ in the descriptions. Again, the rhagidial organs in *Penthaleus* are still regarded as distinct from those of other genera.

Cunliffe (1955) proposed a classification of the Trombidiformes (=Actinedida) in which the superfamily Eupodoidea was first given its modern definition. Cunliffe developed his classification by analyzing other author's systems and by studying the tarsi, gnathosoma, genitalia, palps and body setation. As a result, the Eupodoidea, comprising the families Eupodidae, Penthaleodidae and Rhagidiidae, were defined as mites possessing a small lobe (= the naso) with an associated pair of setae anteriorly on the propodosoma, chelicerae either simple, opposed or partially chelate, simple palps, recumbent striate sensory setae on the tarsi lying in a special membranous area (the rhagidial organs), simple rayed tarsal claws and a pad-like, laterally rayed pulvillus. Other superfamilies were erected by Cunliffe to accommodate families which had previously been included in the Eupodoidea.

In subsequent works, the definition and content of the Eupodoidea remains stable, the differences occurring only in authors' opinions over the division of genera into families and subfamilies.

Fain (1958) described a species of eupodid, *Benoinyssus najae*, discovered in the nasal passage of a snake. Apart from its origin, it was unusual in being the first of a minority of species possessing a pair of opisthosomal trichobothria. This feature was thought by Fain to be

sufficient reason for dividing the family Eupodidae into two subfamilies, the Benoinyssinae and the Eupodinae, members of the latter lacking opisthosomal trichobothria. Despite other species being found which possess opisthosomal trichobothria, this division of the family has not gained general acceptance.

In 1964, Fain's work caused another change in eupodoid classification, but this time to the status of the genus *Protereunetes*. After examining the type specimens of *P. agilis*, the type species of *Protereunetes*, Fain discovered that it was, in fact, a species belonging to the genus *Ereynetes* and he declared *Protereunetes* invalid. Despite the identity of its type, the genus had evolved a definition which encompassed certain eupodoid species. As a consequence of Fain's observation, however, these species, plus those described subsequently which would have been classified in *Protereunetes*, were placed in *Eupodes*. As a result, this latter genus has become a heterogeneous assemblage of species.

From 1963 to 1981, two authors published prolifically on the Eupodoidea. Shiba described many new species and redescribed numerous others which he collected while studying the mite fauna of Malaysia (Shiba 1969, 1971, 1976). However, Shiba included no identification keys in his publications nor did he suggest any changes to or comment on the higher classification or taxonomic position of the Eupodoidea. Strandtmann, the second of these authors, worked extensively in the Arctic and Antarctic regions (Womersley & Strandtmann 1963, Strandtmann 1964-1972) but also in many other areas, including New Zealand (Strandtmann 1981), Hawaii (Strandtmann & Goff 1978) and Europe (Strandtmann & Prasse 1976, Strandtmann & Sømme 1977). He described new species and, where possible, also gave descriptions of the immature stages. He provided keys to families, genera and species, which he

periodically revised, and also tried to clarify the status of early species in an attempt to standardize the use of specific names.

Zacharda (1979) discovered a species of eupodoid which appeared to be close to a rhagidiid but differed by possessing only three and not four pairs of setae associated with the anus (examination of the holotype, however, revealed that four pairs were in fact present) and a neutrichous idiosomal chaetome. Zacharda erected not only a new genus to accommodate this species but also a new family, the Strandmanniidae, with the two characters mentioned above defining it. In the following year, Zacharda (1980) published a monograph of the family Rhagidiidae in which he introduced major systematic changes. The 74 species, 35 of them newly described, were classified into 20 genera, instead of the four which existed before this work. This author also elected to routinely use the subgeneric rank with the aim of making identification of species more easy.

6.2 REVIEW OF THE CLASSIFICATION OF TAXA CURRENTLY INCLUDED IN THE EUPODOIDEA

The following account details the taxonomic position accorded to eupodoid taxa by those authors writing before the establishment of the superfamily and by those who did not utilise the superfamilial rank (Table 2).

The first description of a mite recognized as a eupodoid appeared in the tenth edition of the *Systema Naturae* (Linnaeus 1758). Linnaeus considered mites to be wingless octopod insects and classified them all in the genus *Acarus*. He described one of his species as possessing exceptionally long front legs, which has led workers to consider it to belong to the genus *Linopodes* Koch. In other early records, eupodoids were classified in genera which, in modern classifications, are not part of the Eupodoidea. For example, Hermann (1804) described several species in the genus *Trombidium* which are now recognized as members of the genera *Linopodes*, *Eupodes* and *Penthalodes*.

In 1834, Dugès erected the genus *Megamerus* in the family Trombididae. The defining characters can be paraphrased as follows: palps not raptorial but long and free; body subdivided; coxae fused to venter; femora IV enlarged; larvae hexapod and similar to the adult. Within this genus, Dugès included species which were later reclassified in a number of different eupodoid genera: *M. longipes* is a *Linopodes* species; *M. ovalis* belongs in *Penthalodes* while *M. celer* can be assigned to *Eupodes*. Although *Megamerus* could be regarded as the first supraspecific eupodoid taxon, it has not persisted as it was later found to be a name preoccupied by *Megamerus* Maclean 1827, a genus of insect.

Eupodoids began to be recognized with the work of C. L. Koch, the German acarologist, who described 53 species of eupodoid between 1835 and 1842. He was also the first worker to erect supraspecific taxa which are retained in the modern concept of the Eupodoidea. In 1835, Koch established by indication (Article 12(b)(5), International Code of Zoological Nomenclature (1985)) the first eupodoid genera, namely *Eupodes*, *Linopodes*, *Penthaleus* and *Scyphius*. Later, in 1842, he published accounts of these taxa, classifying respectively 26, 11, 13 and two species in them. *Scyphius* was subsequently acknowledged to be a preoccupied name (*Scyphius* Risso, a genus of fish) and synonymized with *Rhagidia* Thorell by Banks (1900). Koch based his descriptions on the examination of fresh, uncleared material. He principally used the distinguishing characters of body shape, colour patterning, position and lengths of setae and shape and length of the legs; most of which are now known to vary within species. Consequently, Koch's cursory observations are inadequate for identification and, since he did not select type specimens, the identity of most of his species remains unknown. Even early authors acknowledged that Koch's species were generally unidentifiable (Canestrini 1886, Banks 1900). Despite this, however, Koch's figures illustrate that these taxa are undoubtedly eupodoids.

Later, Koch (1841) erected the taxon Scyphiides to contain the genera *Scyphius*, *Penthaleus*, *Linopodes*, *Eupodes* and *Tydeus* with the preoccupied *Scyphius* as type. The description of Scyphiides, however, was so brief that it is regarded as a *nomen nudum* (Oudemans 1937).

The following year, Koch (1842) erected the first eupodoid family which has persisted until the present day, although its composition has been amended. This family, the Eupodides (=Eupodidae) included the genera *Bryobia* (now classified in the family Tetranychidae, superfamily

Tetranychoida), *Scyphius*, *Penthaleus*, *Linopodes*, *Eupodes* and *Tydeus*. In the same work, Koch divided the Acari into four divisions, essentially based on the number of leg segments and the form of the chelicerae. One of these divisions, the Laufmilben (roughly translated as 'running mites'), accommodated the Eupodidae, and was made up of those mites with six leg segments and chelicerae with small chelae. The Eupodidae, given the common name of Prachtmilben ('pretty mites'), were distinguished by possessing two small faint eyes, the prodorsum and opisthosoma clearly separated from each other by a furrow, the palps free and spindle-shaped, the first pair of legs longer than the others and used for both locomotory and sensory purposes. The fact that Koch included *Linopodes* and *Penthaleus* in the family is interesting as neither, in fact, possesses a clear furrow between prodorsum and opisthosoma.

The Eupodidae also appeared in Fürstenberg's general classification of the Acari which was presented at the beginning of his account of the itch mites (Fürstenberg 1861). This system was essentially based on Koch's classification and the Eupodidae were given the same definition and composition as did Koch in his work of 1842.

Mites were further classified by Murray (1877), this time into eight families. His classification possessed components of those of both Dugès (1834) and Koch (1842) but the eupodoid taxa were distributed among several divisions of one of the families, the Trombidiinae. This family was most conspicuously distinguished by the form of the palps which were described as having the terminal segment with some form of opposable 'thumb', sometimes it was like a claw, in others a hair. Eupodoids are clearly misplaced in this family as none has an opposable 'thumb' on the palps. Murray divided the Trombidiinae into two sections, the

Tetranychidae (with the common name of spinning mites) and the Trombidiidae (harvest mites).

The Tetranychidae were described as small, semi-transparent plant-feeders. Amongst these was included the genus *Megamerus* which, as mentioned previously, comprises a mixture of eupodoid genera. From his description and figure, however, it is not clear how Murray defines *Megamerus* as he figures a rhagidiid but gives the presence of long palps, chelate chelicerae and enlarged 'hind thighs' as the principal characters; the latter feature being a diagnostic character for *Eupodes* and *Cocceupodes*. However, the most indicative character to show that Murray is perhaps referring to a rhagidiid is his observation that they are able to spin fine threads of silk. Among the eupodoids, this has only been observed in the rhagidiids (Ehrnsberger 1979).

Murray distinguished the second section of the Trombidiinae, the Trombidiidae, by their brilliant colouring, larger size, velvety appearance and by their predacious habit. The Trombidiidae were further divided, firstly by separating members on the number of their leg segments. Those with six were regarded as equivalent to Koch's Eupodidae. Within this subsection, a further subdivision was made according to whether the prodorsum and opisthosoma were delimited from each other by a furrow. Those genera that possessed such a furrow were given as the genera *Bryobia*, *Petrobia* (now in the family Tetranychidae, superfamily Tetranychoidae), *Eupodes*, *Tydeus*, *Penthaleus* and *Scyphius*. Those lacking a furrow were divided, yet again, into those with exceedingly fine and long anterior legs, comprising the genus *Linopodes*, and those with normal front legs, embracing the newly erected genus *Penthalodes*. Again, there were inaccuracies in the definitive characters as *Penthaleus* does not

possess a subdivided idiosoma. Murray includes another eupodoid species, *Rhagidia gelida*, in the genus *Tydeus* but gives no reason for doing this.

The work of Kramer (1877) provided the basis of a modern classification of mites which has persisted to recent times. He divided them into six families essentially depending on the presence or absence of trachea in the adult and, when present, the position of their openings (the stigmata). One division of the Tracheata, i.e. those that possess tracheae, was the family Prostigmata. These mites have a pair of stigmata at the base of the chelicerae and were divided into 14 subfamilies. One of the subfamilies, the Megameridae, was quoted as being equivalent to Koch's Eupodidae but comprised only the genera *Scyphius*, *Fenthaleus* and *Eupodes*. Kramer defined the Megameridae as those prostigmatids with eyes, an opposable 'thumb' to the palp tarsus and chelate chelicerae. Kramer regarded these three genera to fit the description of the heterogeneous genus *Megamerus* (Dugès 1834). The other genera that Koch had originally included in the family were placed in other subfamilies of Prostigmata; *Bryobia* was placed in the Tetranychidae, *Tydeus* in the Tydidae (later changed to its current spelling of Tydeidae). Despite Kramer's work being the first in which eupodoid taxa in the modern concept were grouped together, this was done only on the basis of arbitrary and inaccurate characters.

Trouessart (1892) divided tracheate mites into those with raptorial palps and styletiform chelicerae and those with tactile palps and chelate chelicerae. The latter were defined as mites possessing a distinct rostrum, free slender palps used for tactile purposes and lacking a 'thumb', chelate chelicerae, a pair of prodorsal eyes and homeomorphic legs used for locomotion. The integument was described as weakly sclerotized, supporting various types of setae and sometimes brightly

coloured. The larvae of this group are like the adults, all stages being free-living and active. Trouessart classified the Bdellidae in this group which itself was divided into two subfamilies distinguished from one another by the form of the palps and chelicerae. The Bdellinae were characterized by long, elbowed palps and clawed chelicerae while the Eupodinae possessed medium or short palps with four segments and chelicerae with chela more or less developed. Other observations of eupodines given were the legs being used for locomotion and ending in two claws, rarely in one, the weakly sclerotized integument and the setae being leaf-, feather- or rosette-shaped. The genera classified in the Eupodinae were *Tydeus*, *Halotydeus*, *Ereynetes*, *Linopodes*, *Megamerus*, *Notophallus*, *Scyphius*, *Noerneria*, *Scyphiodes* (Karpelles 1891), *Eupodes*, *Penthaleus*, *Pronematus*, *Nanorchestes* (Tops & Trouessart 1890) (now classified in the family Nanorchestidae, superfamily Pachygnathoidea), *Alychus* and *Michaelia* Berlese (now in the family Pachygnathidae, superfamily Pachygnathoidea).

Berlese (1893) placed the Eupodidae in the order Prostigmata, suborder Trombidides, which comprised the terrestrial members of the order. Eupodids were defined as having an unornamented body, the larva resembling the adult, an inconspicuous penis, chelate chelicerae and simple palps. The following genera were included: *Tydeus*, *Ereynetes* Berlese (now classified in the family Ereynetidae, superfamily Tydeoidea), *Noerneria* Canestrini 1886 (= *Rhagidia*), *Eupodes*, *Linopodes*, *Penthaleus*, *Halotydeus* Berlese 1891 (a current member of the Eupodoidea), *Notophallus* Canestrini 1886 (= *Penthaleus* Koch), *Pronematus* Canestrini (now in the family Tydeidae, superfamily Tydeoidea) and *Eupalus* Koch (= *Cunaxoides* Baker & Hoffmann 1948, family Cunaxidae, superfamily Bdelloidea).

In 1904, Oudemans put forward the case for not separating the Eupodinae from the Trombidiidae. Some authors, he stated, wanted to separate them on the basis of the lack of an opposable palpal 'thumb'. Oudemans did not regard this character alone to warrant separation from other trombids. He attributed the following character states to the Eupodinae:

- 1) Body weakly sclerotized, with or without weak shields.
- 2) Larvae free-living, resembling adults.
- 3) Male without penis.
- 4) Chelicerae not chelate.
- 5) Chelicerae short, with one falciform and one membranous digit.

Trägårdh (1910), in his study of the mite fauna of Sweden, assigned species to families. He divided the family Trombidiidae into a number of subfamilies, the Eupodinae was one of them and was defined by the following features:

- 1) The larvae resemble the adults (apart from the number of legs).
- 2) Penis absent.
- 3) Chelicerae with claws or with chela.

The genera this definition encompassed were *Tydeus*, *Rhagidia*, *Eupodes*, *Fenthalodes* and *Fenthaleus*.

Oudemans (1923) published a revised classification introducing several new rankings. He divided the suborder Trombidiformes into supercohors and cohors. The Supercohors Stomatostigmata (=supercohors Prostigmata) was divided into the cohors Cursoria which included the families Bdellidae, Eupodidae, Tydeidae, Cunaxidae, Labidstommidae Oudemans 1906 and Rhagidiidae. No definitions were given however.

Vitzhum (1941) published an extensive work on mite classification in which members currently classified in the Eupodoidea were placed in the cohort Prostigmata, subcohort Eleutherengona Oudemans 1909 (= mites where the habitat of the larva is the same as the adult, and does not have a parasitic mode of life). He did not use the category of superfamily but classified the genera into families, although without giving definitions. The membership of the eupodoid families in Vitzhum's work is essentially the same as is currently accepted. The family Eupodidae was said to comprise the genera *Eupodes*, *Cocceupodes*, *Protereunetes* Berlese 1923 (now invalid, Fain (1964)), *Linopodes*, *Protacarus* Hirst 1923 (fossil) (now considered to belong in the Pachygnathidae). The family Penthaleidae Oudemans 1922 contained the genera *Penthaleus* and *Halotydeus*. The family Penthalodidae Thor 1933 comprised the genera *Penthalodes* (= *Penthaleus* Berlese 1891 = *Chromotydeus* Berlese 1903), *Tectopenthalodes* Tragardh 1907, *Stereotydeus* Berlese 1901. The genera *Rhagidia* and *Coccorhagidia* were classified together in the Rhagidiidae Oudemans 1922. Although the discovery of rhagidial organs had been documented for several years at this time, Vitzhum did not refer to them in the context of a unifying character merely referring to their presence in the description of *Rhagidia gelida*.

The first workers to use the presence of rhagidial organs to unify the taxa now classified in the superfamily Eupodoidea were Baker & Wharton (1952). These authors felt that certain families could form the basis of superfamilies but, as they regarded the usage of this category to be still in its formative stage, made no attempt to use superfamilial nomenclature or to define them. Baker & Wharton considered many of the characters used by early authors in their classifications, for example, position of stigmatal openings, habitat, shape and form of the palps,

gnathosoma, chela, propodosomal pseudostigmata (=bothridia) and pseudostigmatid organs (=trichobothria). However, for the first time, the presence of rhagidial organs is used to key out the families Eupodidae Koch, Penthalodidae Thor (penthaleid species were included in this family) and Rhagidiidae Oudemans; in practice, those now classified in the superfamily Eupodoidea.

6.3. CURRENT SYSTEMATIC POSITION OF THE EUPODOIDEA

The primitive acarine body has subsequently undergone such diverse modification that it is often difficult to find unifying characters, especially for higher taxa. Historically, there have been many changes in classification and there is still disagreement and uncertainty over the relationships between taxa. There is no consensus even over the phylogeny of the mites, various authors favouring a mono-, di- or paraphyletic origin (Lindquist 1984).

In the most recent comprehensive classifications of the Acari (van der Hammen 1972, Krantz 1978, Kethley 1982), the Eupodoidea are classified in the Acariformes, as summarized in Table 3.

The characters used to define the various taxonomic categories in relation to those possessed by eupodoids are considered below. Citations of these three authors will always refer to the publications quoted in Table 3 and so dates will not be subsequently given.

Acariformes/Actinotrichida

This is generally regarded as the most taxonomically and biologically diverse order of mites, members having adapted to terrestrial, freshwater and marine habitats and to fungivorous, herbivorous, predacious and parasitic feeding habits. The fundamental characteristic of this order is the presence of optically active actinopilin in the setae (Grandjean 1935a, 1947a), the possession of which is demonstrated in eupodoids by Ehrnsberger (1974).

Table 3. The systematic position of the Eupodoidea in recent classifications.

	VAN DER HAMMEN (1972)	KRANTZ (1978)	KETHLEY (1982)
<u>Subclass</u>	Acarida	Acari	-
<u>Order</u>	Actinotrichida	Acariformes	Acariformes
	(Superorder)*		
<u>Suborder</u>	Actinedida (Order)*	Actinedida	Prostigmata
<u>Supercohort</u>	-	Promatides	-
<u>Cohort</u>	Bdellina (Suborder)*	Eupodina	Eupodina
<u>Superfamily</u>	Eupodoidea	Eupodoidea	Eupodoidea

* alternative rankings used by author

Van der Hammen prepared a list of characters in addition to the optical qualities of the setae to distinguish the Actinotrichida from the other acarine superorder/order, the Anactinotrichida. Some of these characters refer to the assumed primitive condition of the group and are not possessed by eupodoids but the majority are present. For example, the presence of a podocephalic canal, a sejugal (=disjugal of other authors) furrow, idiosomal trichobothria and the absence of free coxae, a dorsal cheliceral lyrifissure and a palpal apotele.

Krantz gives no diagnosis but keys out the orders. The following key characters qualify the Eupodoidea for Krantz's concept of this taxon: the lack of visible stigmata posterior to coxae II; propodosomal sensory organs which are simple sensilla; the presence of a pair of podocephalic canals and coxae fused to the ventral body wall forming a coxisternal region delimited by epimera.

Kethley acknowledges the diversity in body morphology within this order and deals with its characteristics by giving an extensive account of a hypothetical primitive acariform condition. According to this definition, eupodoids possess many primitive characters:

- the palps have five segments and lack a pretarsus;
- the cheliceral bases are separate and capable of independent motion;
- podocephalic canals open at the base of the chelicerae;
- a dorsosejugal furrow usually divides the body;
- the coxae are completely fused to the ventral body wall;
- the legs are generally homeomorphic;
- the leg pretarsus bears paired claws and an empodium;
- optically active tactile setae occur on the idiosoma and appendages;

the life cycle is unmodified comprising the egg, inactive octopod prelarva, active hexapod larva, three octopod nymphs and adults; sperm transfer is *via* spermatophores;

both eugenital setae and genital papillae occur.

Exceptions, however, do occur as, in some genera, the sejugal furrow is absent or is represented by a faint differentiation of the integument, both neo- and hypotrichy occur, leg I is sometimes markedly elongated and slender, while the femur of leg IV can be greatly enlarged. Derivations also occur, for example the primitive chelate-dentate condition of the chelicerae is much reduced in most genera, the prodorsum typically has two pairs of both true setae and trichobothria (see section on Eupodoidea below for discussion of this) instead of, respectively, six and two pairs primitively, while the chaetome of the opisthodorsum is also reduced, having only three pairs of lyrifissures and five transverse rows of setae and not six and nine respectively. In addition, the basi- and telofemur of eupodoids are not separate segments; although on legs III and IV they sometimes appear to be so externally, their musculature is shared. Finally, chemoreceptors are not present on all genera, tibiae and tarsi.

Prostigmata/Actinedida

Van der Hammen gave seven characters by which to distinguish actinedid mites, conceding that not all were possessed by every member. Five of these characters apply to eupodoids: a rostral tectum is absent, two pairs of prodorsal trichobothria are present, a gastrontal sclerite is absent, femora solenidia can be present and the median claw of the apotele is replaced by an empodium (cf. Kethley who regarded this as a primitive ordinal character).

Both Krantz and Kethley stress the diversity in morphology and habit of this taxa compared with the other acariform suborders and give accounts of the way in which modifications occur. Neither, however, provides a set of diagnostic characters to unite the members.

In Krantz's key to orders and suborders, the Eupodoidea are identified as actinedids by virtue of possessing simple palps with four recognizable palpal segments, stigmatal openings located between the cheliceral bases, clawed pretarsi, rayed or pad-like empodia, propodosomal sensory organs and a weakly sclerotized body. Comparing characteristics of eupodoids with Kethley's definition of prostigmatids indicates that eupodoids have undergone relatively little modification and retain many features of the generalized acariform plan - their palps are simple, neither reduced nor raptorial, the chelicerae are more or less chelate and are never fused, the sejugal furrow is evident in most genera, there is no reduction in the number of immature stages while, with few exceptions, eupodoids feed on lower plants or are free-living predators, habits now found only in a minority of prostigmatids. Like most other members of the suborder, though, anamorphosis is partially regressed in eupodoids, no segments being added after the adanal in the protonymph.

Eupodina/Bdellina

Van der Hammen does not give diagnostic characters but lists the members as the superfamilies Cunaxoidea (=Bdelloidea), Tydeoidea, Halacaroidea and Eupodoidea.

The accounts of the cohort by both Krantz and Kethley reflect the diversity of the group and raise the possibility of it being a heterogeneous assemblage. It is especially difficult to be certain of the correct inclusion of the halacaroids as they lack many of the diagnostic

characters even of the order (Macquitty 1984); these are presumed to have been lost during the adaptation to a mainly marine way of life.

Krantz gives a range of character states which members of this cohort possess. Those of the eupodooids which qualify them for inclusion are presence of post-cheliceral peritremes and stigmata, chelate or modified chelate chelicerae, simple palps with four segments and solenidia of tarsus I appressed to the segment. He includes the same superfamilies as van der Hammen in the cohort.

Kethley includes a fifth superfamily, the Nematalycoidea, and consequently, although it largely agrees with Krantz, his definition of the cohort is somewhat wider. The Eupodoidea, though, possess the same qualifying characteristics as those given by Krantz but with the addition of the presence of genital papillae and eugenital setae.

Eupodoidea

Again, van der Hammen gives no diagnosis.

Krantz's definition of the superfamily contains a number of inaccuracies:

- a) he states that the naso (=epivertex) bears a pair of setae, but, in fact, this pair (the internal vertical setae) can be located on, at the base of or just posterior to the epivertex.
- b) only one pair of prodorsal trichobothria is reputed to occur, but the internal vertical setae, can be seen to have enlarged insertion pits (Fig. 20) and should be regarded as trichobothria.
- c) Krantz's description of the chelicerae is misleading as the movable digit is never needle-like, always being hooked to a greater or lesser extent.

d) claws are always present on tarsus I but are sometimes much reduced.

e) two genital acetabula (=papillae) are only found, never three.

Kethley gives a generally comprehensive definition of the superfamily, but errors are included. He states that there is no post-larval addition of opisthosomal segments (evidence suggests that one is added in the protonymph, see section 11), accepts the possibility of three pairs of genital papillae occurring, while, he considers the leg femora to be divided into two segments when, in fact, they are undivided in certain genera and only partially so in others.

7. STUDY OF THE EXTERNAL MORPHOLOGY OF THE EUPODOIDEA

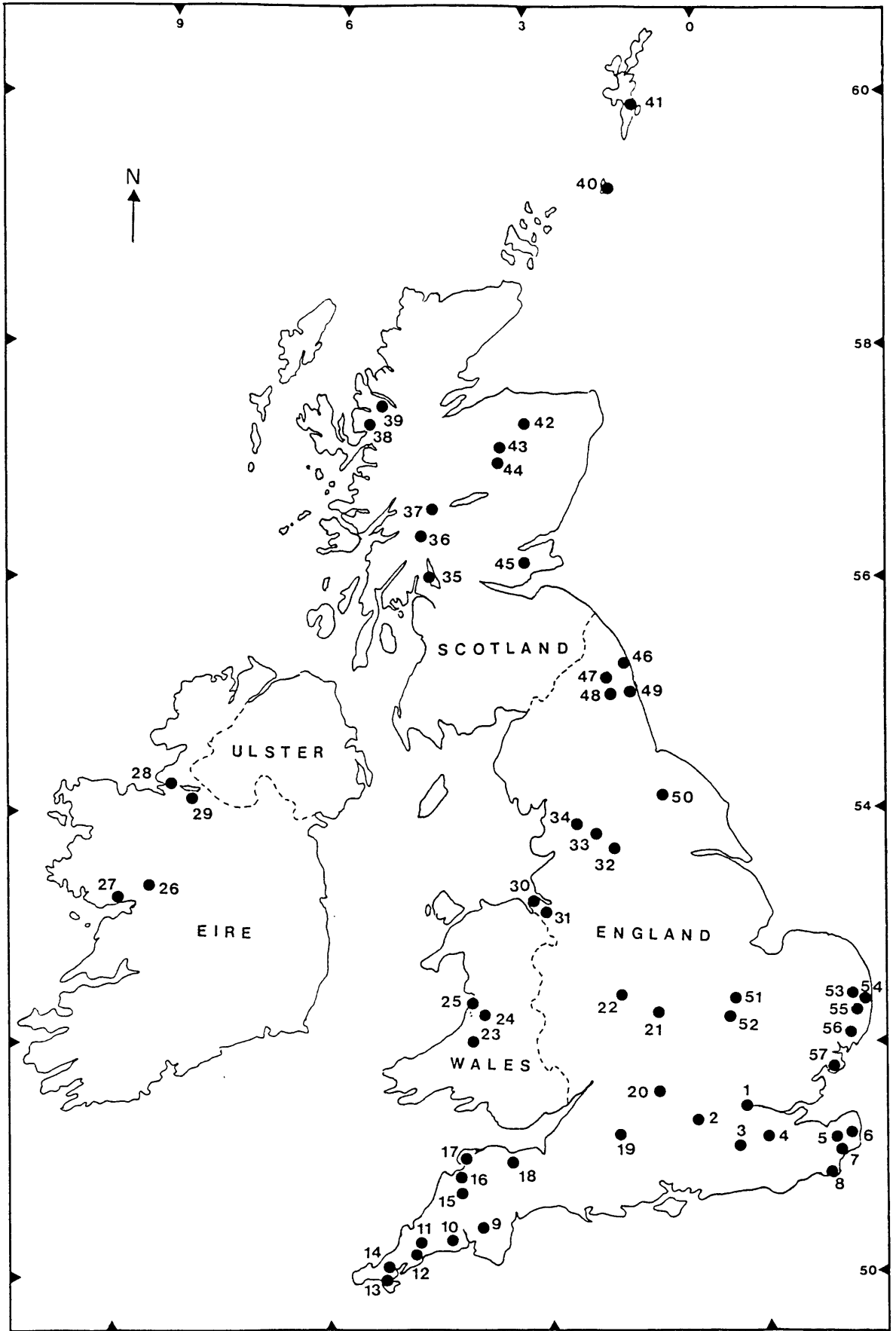
7.1 MATERIAL EXAMINED

The majority of the specimens used in this study was obtained from an extensive collection of British eupodoids made by the author during 1980 and 1981. From the outset, the aim of the collecting programme was to maximise the chances of obtaining a representative collection for taxonomic studies. Emphasis was, therefore, placed on sampling a wide range of habitats and localities. Details of localities are given in Fig. 1.

The above material was supplemented by specimens from collections of unsorted soil samples housed in the Arachnida and Myriapoda Section of the British Museum (Natural History) and by the loan of specimens from other workers (see acknowledgements).

Fig. 1. British Isles: principal collection sites.

- | | |
|------------------------------------|-----------------------|
| 1. South Kensington | 36. Tainish |
| 2. Windsor Forest | 37. Rannoch Moor |
| 3. Whiteland Downs, Chobham Common | 38. Loch Kishorn |
| 4. Westerham | 39. Loch Maree |
| 5. Sandwich Bay | 40. Fair Isle |
| 6. Canterbury | 41. Lerwick |
| 7. Folkestone | 42. Craigellachie |
| 8. Dungeness | 43. Grantown-on-Spey |
| 9. Cornwood, Higher Piles Copse | 44. Cairngorms |
| 10. Saltash | 45. Abernethy Forest. |
| 11. Bugle | 46. Alnmouth |
| 12. St Austell | 47. Rothbury |
| 37. Tynemouth | 48. Bolam Lake |
| 42. Walberswick | 49. Tynemouth |
| 13. Gweek | 50. North York Moors |
| 14. Goonhilly Downs | 51. Peterborough |
| 15. Torridge | 52. Woodwalton Fen |
| 16. Northam Burrows | 53. Westleton Heath |
| 17. Appledore, Branton Burrows | 54. Walberswick |
| 18. West Bagborough | 55. South Wold |
| 19. Savernake Forest | 56. Hollesley Common |
| 20. Wytham Woods | 57. Colne Point |
| 21. Hinkley | |
| 22. Cannock Chase | |
| 23. Tregaron | |
| 24. Capel Bangor, Rheidol Forest | |
| 25. Borth | |
| 26. Monivea | |
| 27. Galway | |
| 28. Sligo | |
| 29. Lough Gill | |
| 30. Parkgate, The Wirral | |
| 31. Ellesmere Port | |
| 32. Ilkley Moor | |
| 33. Boltons Abbey | |
| 34. Wigglesworth | |
| 35. Loch Lomond, Inchcailloch | |



7.2. METHODS

7.2.1. Collection of specimens

Unlike larger arachnids, for example spiders and harvestmen, soil and litter mites are not easily collected by visual and hand methods such as grubbing and sweeping. Instead, they are most efficiently obtained by collecting samples of their habitat which are subsequently subjected to an extraction process (see section 7.2.2). In this study, each sample was placed in a heavy gauge 60 by 45cm polythene bag immediately after collection, filling it to not more than a third of its capacity. The bag was then closed, ensuring that some air was also trapped inside, with an elastic band carrying a numbered identity tag. Great care was taken to keep disturbance of the samples to a minimum during the extraction process, so as to reduce the risk of the interstices becoming blocked and thereby preventing the mites' escape.

Soil blocks, approximately 20 by 14 by 14cms, were cut and removed using a small garden spade. Samples of fungi, lichens and moss-mats were cut with a sharp knife, while loose material such as shore debris and decomposing wood was simply picked up and placed in a polythene bag.

Specimens were also sought in habitats where there was no accumulation of detritus, such as rocky areas and caves, that could not be sampled in the above way. Time was spent searching rocks, walls and crevices; any eupodoids that were found were transferred to tubes of 70% methanol using a moistened paint-brush or a small pooter.

A portable suction sampler (the 'Univac', made by Burkard Manufacturing Co. Ltd) was used to collect large numbers of living specimens from surface habitats, particularly for use in scanning electron microscopy. In the form supplied, the 'Univac' comprises a two-stroke

engine powering a vacuum unit and a collecting chamber, all of which are mounted on a ruck-sack frame and carried as a back-pack (Figs 2 & 3). The collection chamber is fitted with a cover maintained in place by the vacuum created when the machine is running. About two metres of a six centimetre diameter plastic suction tube, held open by an integral spiral of wire, extends from the centre of this cover. Specimens are sucked up through this tube and into the collection chamber. This system, however, was found not to be suitable for collecting mites (or other small arthropods) as specimens were damaged during the long journey through the suction tube. Also, many become trapped in the condensation that invariably forms on the inside of the tube. The machine was, therefore, adapted (Fig. 2) so that the specimens could pass directly from their habitat into a 25 by 10cm, removable cotton bag (demonstrated in Fig. 3). This was achieved as follows.

The suction tube was shortened by about 45cms and the free end joined to a 90cm length of 6cm diameter plastic drain-piping (collecting tube) by means of a plastic pipe connector. The cotton bag was inserted into the collecting tube, its opening folded back over the tube and held in position by a plastic collar. A piece of one centimetre wire mesh was bent over the end of the collecting tube to exclude large particles, such as leaves, from the sample. After sampling, the bag was extricated by disconnecting the collecting tube and removing the mesh and collar. Before disconnection, the collecting tube is held with the free end uppermost to prevent the contents of the sample bag from falling out in the absence of the vacuum. Apart from preventing loss of specimens for the reasons mentioned above, these adaptations have other advantages. For example, collecting bags can be replaced without either taking or

turning the machine off, while the rigid collecting tube gives better control during sampling than the flexible suction hose.

Sample bags containing specimens were stored in 30cm square plastic bags prior to sorting in the laboratory. Mites were extracted by carefully turning the bags inside out over a 10cm diameter petri dish half-filled with water. Surface tension helps to keep the mites afloat but also impedes their activity sufficiently to make capture easier.

Samples were examined using a Wild M4 binocular stereomicroscope at a magnification of about X50 and specimens removed by lifting them out on the tip of a minuten pin mounted on a match-stick.

Fig. 2. Adapted 'Univac' portable suction sampler:

a = two-stroke engine, vacuum unit and collection chamber mounted on ruck-sack frame, b = collection chamber, c = collection chamber cover and associated suction tube with integral wire spiral, d = pipe connector, e = collecting tube, f = cotton sample bag, g = plastic collar, h = wire mesh cover.

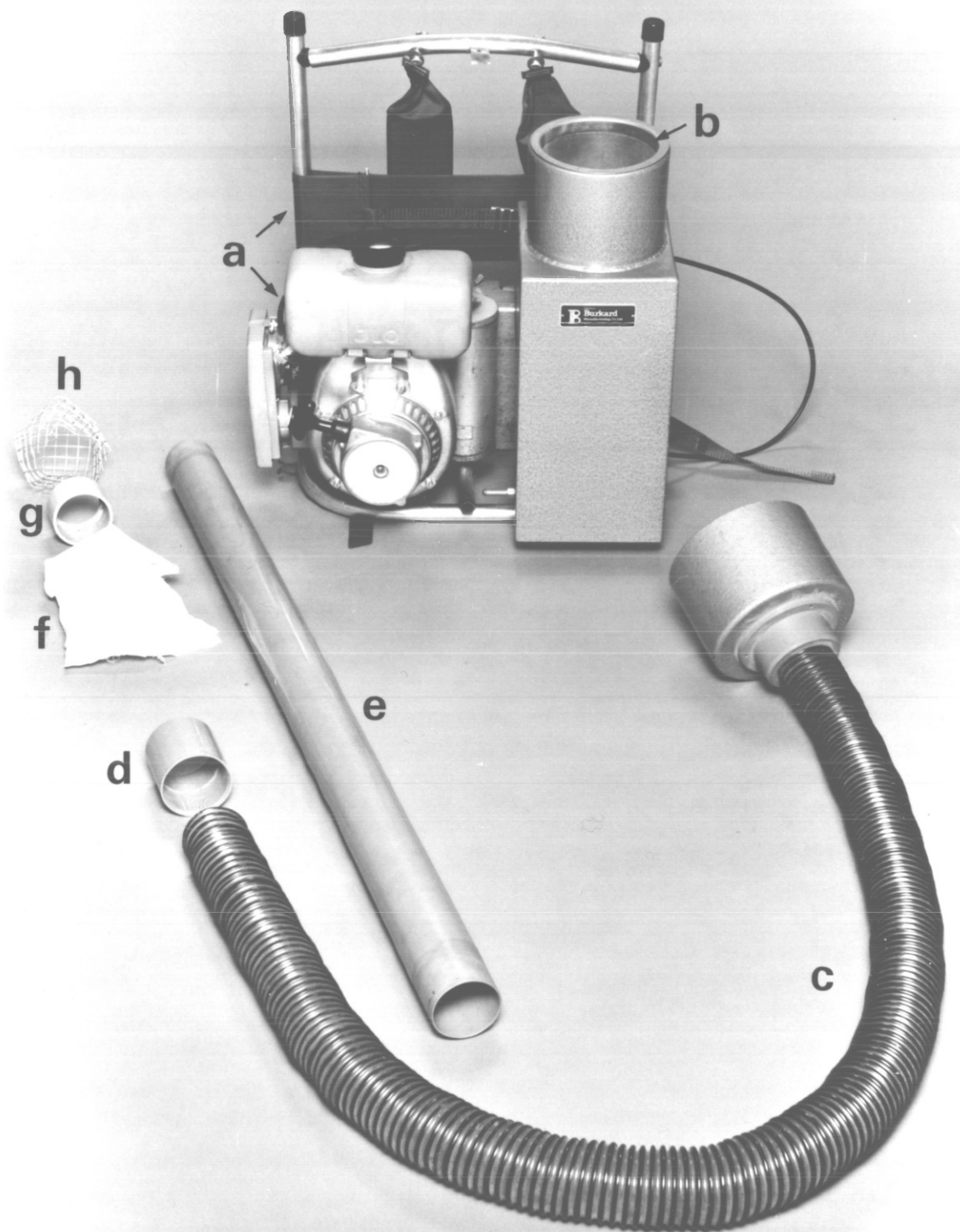


Fig. 3. 'Univac' portable suction sampler in operation. Sample bag arrowed.



7.2.2 Extraction of specimens from habitat samples

Eupodoid mites, together with other mesofauna, were extracted from habitat samples using an adaptation of the funnel desiccation method of Berlese (1905). The apparatus used in this study is the modified version of MacFadyen's high-gradient system with air conditioning devised by Parry (1976). This method was chosen for use in the present study because of its reported efficiency for extracting prostigmatid mites (Aucamp, Loots & Ryke 1964, Wood 1965, Edwards & Fletcher 1967) and also because many samples could be processed at once, unlike other methods such as floatation.

The extraction apparatus comprises six units (Fig. 4), each capable of processing 20 samples. Each unit consists of an insulated wooden cabinet divided into two parts by a horizontal baffle-board so that the upper part accounts for about one third of the cabinet's capacity. Access is gained to the lower section *via* removable doors at the front and back and to the upper part by a lid pivoted at front and back. Each cabinet houses four rows of five spun aluminium funnels, each of which is 15cms in diameter by 26cms high with a nozzle diameter of 12mm (Fig. 5a). The steep smooth sides of the funnels provide no refuges to trap the specimens. Each funnel rests in a tapering hole in one of four wooden battens running from side to side. The samples are held in spun aluminium cylinders, 12.5cms in diameter and 9cms deep with a 2mm mesh sieve resting in the base (Fig. 5b). The cylinders fit closely through holes in the baffle-board dividing the cabinet and are kept in position by four lugs. The cylinders rest within, but do not touch, the tops of the funnels; an arrangement which is said to reduce the risk of condensation forming in the funnels and so trapping specimens.

Fig. 4. Apparatus for the extraction of specimens from habitat samples:

- (a) six units of extraction apparatus; one with lid raised, four with doors removed. Section of circulation system insulated with 'Armafex' arrowed.
- (b) view inside the upper compartment of one unit showing light bulbs in lid and cylinder containing sample (raised). Cap-board cover arrowed in black, thermostat arrowed in white.

a



b

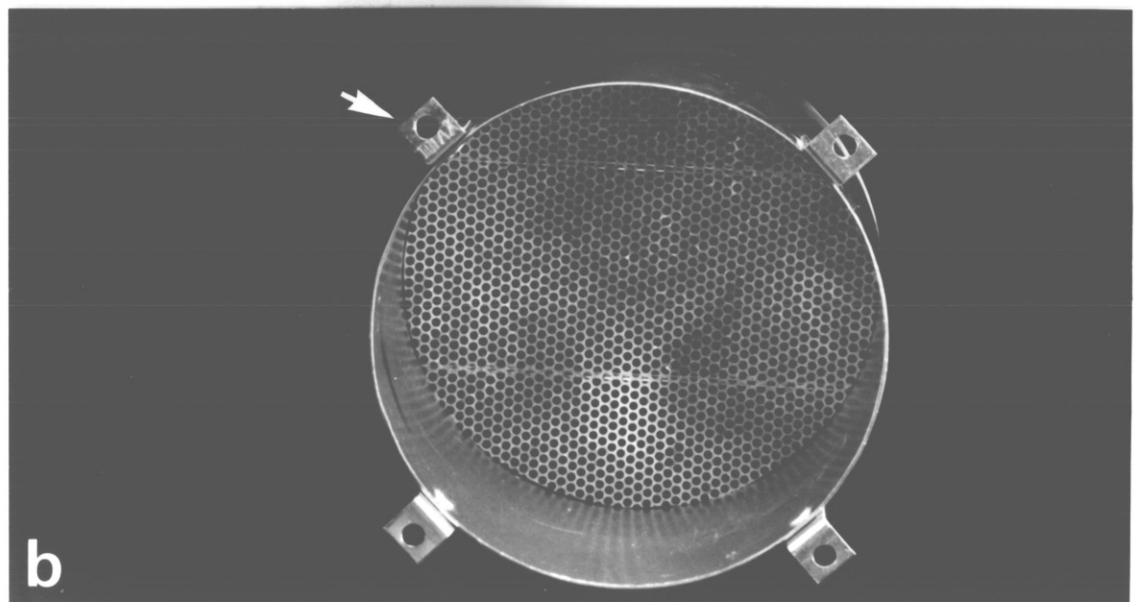


After the samples have been loaded, two cape-board covers per unit are laid on top of the baffle-board and over the cylinders. Each cover has 10 holes, corresponding to the locations of the cylinders. The holes overlap the circumference of the cylinders by about 2.5cms so as to minimize heating of their walls. Heat is provided by four rows of five 20 watt electric light bulbs fixed in the roof of the lid. The air in the lower compartment is cooled by a refrigerated solution of ethylene glycol circulating through eight sections of car radiators located between the funnels and connected by 10mm diameter polythene tubing. All six cabinets are linked by insulated polythene tubing to form one continuous system. The solution is cooled when it passes through a Searle Liquid Cooler HX-40 and circulated by a Stuart Turner Ltd pump, model number 90/K2792/894. Two fans suspended at the level of the funnel nozzles distribute the cool air throughout the lower compartment. The temperatures of the two parts of the cabinets are thermostatically regulated so that the gradient can be controlled.

For the most part, specimens were extracted into about 2cms of 70% methanol contained in glass tubes (7.5 x 1.4cms) attached to the funnel nozzles by a short piece of polythene tubing. Although the non-repellant picric acid is more efficient than alcohol for the extraction of micro-arthropods, it has the disadvantage of colouring specimens and making them difficult to clear. The extraction method used in this study was found to have an adequate level of efficiency (see below) and so the alcoholic preservative was preferred. If live mites are required, the alcohol can be replaced by distilled water.

Fig. 5. Details of extraction apparatus:

- (a) two funnels resting in battens with sections of car radiators on either side. A fan is located beneath batten, in lower compartment. Polythene tubing through which anti-freeze solution circulates arrowed in black, collecting tube containing alcohol preservative arrowed in white.
- (b) View inside cylinder showing basal mesh. One of the four lugs which maintain cylinder in position arrowed.



Prior to sorting the extracted material, the samples were emptied into 10cm diameter petri dishes with a 5mm grid etched into the base. It was examined, at about x50 magnification, using a Wild M4 stereomicroscope. The squares were individually scrutinized in horizontal and vertical lines to ensure that, as far as possible, no specimens were missed. Specimens were removed using a small spatula, made from the flattened point of a fine entomological pin, and stored in 70% methanol in glass vials until required for study.

Funnel desiccation methods depend on the ability of the animals to respond negatively to increases in light intensity, temperature and drying so that they ultimately move out of the sample. As most of the mite population inhabits the upper layers of the substrate, samples were inverted when loaded into the cylinders to reduce the distance for them to travel. Care was, again, taken not to compress the samples to prevent the mites being trapped.

A suitable gradient for the extraction of eupodoid mites was found to be 18-20°C above the samples and 8-12°C below. To confirm that they were indeed being efficiently extracted, samples from various habitats which had already been subjected to funnel desiccation were reprocessed using a sophisticated floatation technique (Thind & Griffiths 1979). It was found that, while in most habitats, particularly sandy and clay soils, a number of eupodoids had not escaped from the sample, they did not occur in great numbers nor, and more importantly for a qualitative study, did they represent taxa or life stages not found amongst specimens extracted by the funnel method.

7.2.3. Preparation of specimens for light microscopy

Temporary preparations

Eupodoid mites are best studied in temporary preparations where specimens can be orientated into any position for examination with the least distortion. Specimens were mounted in 50-60% lactic acid in glass cavity slides and then covered with 19mm diameter '0' gauge coverslips. Slides with 9, 11 and 15mm diameter cavities were used for respectively small, medium and large mites. Lactic acid softens and clears specimens, the speed of the processes being accelerated by gentle warming. The lightly sclerotized bodies of eupodoids, in particular those of immatures, are apt to burst if the preparation is warmed too fiercely. Five to 15 minutes on a hot-plate at a temperature range of 50-60°C was sufficient but, in most cases, preparations would clear if left overnight at room temperature.

Selective stains were sometimes used to make structures more easily discernable: (a) Lignin pink emphasised the more chitinised parts of the body (Evans & Browning 1955) and was used in the following mounting medium:

60% lactic acid	60 parts
Glycerine	40 parts
Lignin pink	one drop

(b) The presence of actinopilin was highlighted by mounting material in warm lactic acid saturated with iodine (Grandjean 1935a).

Permanent preparations

When descriptions had been completed, permanent preparations were made using Hoyer's medium, which is made up as follows:

Distilled water	50ml.
Crystalline gum arabic	30g.
Chloral hydrate	200g.
Glycerine	20ml.

The resulting solution is filtered through bolting silk to remove impurities.

Specimens transferred from temporary mounts were first rinsed thoroughly in 70% methanol to prevent residual lactic acid causing subsequent crystallization of the Hoyer's medium. Each specimen was placed on a small drop of mountant in the centre of a clean flat glass slide, covered with a 13mm diameter '0' gauge coverslip and orientated to the required position by gently moving the coverslip. The preparation was then heated for five minutes on a hot-plate at a temperature of 60-70°C. This rapid heating causes the mountant to expand which, in turn, extends the appendages. Drying was completed in an incubator at 40°C for 10 days. Hoyer's medium is hygroscopic and it is therefore necessary to seal the preparation to prevent water uptake from the atmosphere and eventual breakdown of the mountant. In this study, two layers of Glyptal were applied to the edge of the coverslip with a fine paintbrush and using a slide turntable.

All slide preparations were examined under a Zeiss Standard WL compound microscope, mostly under phase contrast. Measurements were made using a graticule incorporated into one of the oculars of the microscope. All drawings were made with the aid of a *camera lucida*.

7.2.4. Preparation for scanning electron microscopy

Specimens examined by scanning electron microscopy were prepared in such a way as to prevent shrinkage and distortion of the tissues. Critical point and freeze drying methods were tried but the latter was found to produce more consistently good results and so was used to prepare the bulk of the specimens photographed.

In preparation for freeze drying, specimens were pre-frozen for 24 hours in a domestic deep-freeze. Mites preserved in alcohol were first passed through several changes of distilled water. The frozen specimens were subsequently transferred to an Edwards Modulyo freeze dryer. Sublimation drying under vacuum (primary drying), during which the specimens are at the bottom of the freeze dryer chamber, took 48 hours, while desorption of remaining moisture (secondary drying) occurred at the top of the chamber and lasted for 36 hours.

The freeze-dried specimens were fixed to aluminium SEM stubs previously coated with a thin layer of Araldite. The mites were transferred using a minuten pin embedded in the end of a matchstick; they would adhere to the pin on gentle contact and could then be lowered onto the stub in the required orientation. Finally before scanning, the specimens were sputter-coated with a 15 μ m thick layer of a gold-palladium mixture in a Techne sputter-coater and examined using a Hitachi S800 scanning electron microscope.

7.3 DESCRIPTION OF THE EXTERNAL MORPHOLOGY OF THE EUPODOIDEA

This account is based on examinations of cleared, temporarily mounted specimens of the British eupodoids collected during the present study and is enhanced by scanning electron micrographs (found at the end of this section, p. 95-126). The account is complemented with morphological details of taxa not found in the British fauna. Sexual dimorphism in this superfamily is only marked in the genitalia; details of external features, therefore, apply to both males and females.

With the exception of the genitalia, which are discernible in macerated specimens, internal structures are not used here as taxonomic characters. Details of internal structures can be obtained from Ehrnsberger (1979, 1984) and Zacharda (1980).

Although the account refers to adult mites, most aspects also apply to the immature stages. The distinguishing features of immatures are given in Section 7.3.9.

7.3.1 Terminology

Grandjean (1964) describes two systems for naming features: notations are objective names which refer to homologous organs, whereas designations are arbitrary labels and used when homologies cannot be confirmed.

Morphological studies, as well as observing and describing structural features, should also be concerned with the identification of homologous structures since this facilitates easier comparison between taxa. Attempts, therefore, have been made here to homologize structures observed in the Eupodoidea with those in other superfamilies and to apply where possible, a standardized notation system of nomenclature (see also

Section 11). For the most part, and following the example of other authors, the nomenclature used in this account has been taken from the many systems devised by Grandjean. When a term is first referred to, its notation or designation is given in brackets afterwards. The terms used in this account of morphology may differ from those used by other authors in describing eupodoids. For clarification, the various systems are compared in Table 4.

Terms used to describe the position of structures in this account conform to certain conventions that are demonstrated in Fig. 6. If the appendages of the specimen are imagined to be held at right angles to the body, they have an anterior and a posterior face, respectively termed anterolateral and posterolateral (= anteroaxial and posteroaxial of Griffiths (1977)). The setae of the former are notated with a prime (') and the latter with a double prime ("). A second convention used refers to the mite in its natural position, that is with the first two pairs of legs forwardly and the last two backwardly directed. Paraxial refers to structures closer to the longitudinal axis of the body, while antiaxial features are furthest from this plane. In this study, the anterolateral/posterolateral system is used when naming setae so that homologues can be compared, whereas paraxial and antiaxial are used to describe relative positions. Setae usually occur in pairs; if both members of a pair are being referred to, the notation is always bracketed, when a single seta is discussed, brackets are omitted.

In certain eupodoid genera, the postlarval stages become progressively neotrichous, the adults having a setal complement far exceeding the basic plan described below (see section 10.1.2). This makes the certain homologizing of setae impossible. In these cases, aspects of chaetotaxy obtained from the examination of larval forms are described in Section 11.

Table 4. Comparison of terms used by various authors for the external morphology of eupodoid mites.

- no term applied, = same term applied as previous author,

* from Strandtmann & Prasse (1976).

PRESENT STUDY	STRANDTMANN (1967/1971)	ZACHARDA (1980)	BOOTH <i>et al</i> (1985)
Gnathosoma;			
subcapitulum	hypostome	-	-
adoral setae	internal/apical rostral	subterminal hypostomal	-
subcapitular setae; (<i>sbc</i> ₁) (<i>sbc</i> ₂)	basal rostral apical/external rostral	basal hypostomal	-
Chelicerae			
<i>cha</i>	-	proximal cheliceral seta	-
<i>chb</i>	-	distal cheliceral seta	-
Supracoxal setae	-	supraepimeral	-
Idiosoma - dorsum;			
sejugal furrow	furrow/suture	disjugal	-
naso	epivertex	naso	epivertex
Opisthosomal setae			
<i>c</i> ₁	internal humeral	=	=
<i>c</i> ₂	external humeral	=	=
<i>d</i> ₁	first dorsal	=	=
<i>e</i> ₁	second dorsal	=	=
<i>f</i> ₁	internal lumbar	=	=
<i>f</i> ₂	external lumbar	=	=
<i>h</i> ₁	internal sacral	=	=
<i>h</i> ₂	external sacral	=	=
- lyrifissures			
<i>ia</i>	-	ly1	<i>ia</i>
<i>im</i>	-	ly2	<i>im</i>
<i>ip</i>	-	ly3	<i>ip</i>
Idiosoma - venter;			
Podosomal setae		epimeral	
<i>1a</i>	inner coxal I	-	-
<i>1b-c</i>	-	-	coxal I 2-1
<i>2a</i>	inner coxal II	-	coxal II
<i>3a</i>	inner coxal III	-	-
<i>3b-d</i>	-	-	coxal III 3,1,2
<i>4a</i>	inner coxal IV	-	-
<i>4b-c</i>	-	-	coxal IV 2-1
Genital region			
eugenital setae	internal genital	eugenital	internal genital
genital setae	external genital	progenital	external genital
aggenital setae	paragenital	=	=
genital papillae	internal knobs/suckers	progenital knob	genital papillae
Anal region			
pseudanal setae	anal	=	=
adanal setae	anal	=	-
lyrifissure <i>ih</i>	-	ly4	<i>ih</i>
Legs			
famulus tarsus I	stellate seta	=	stellate famulus
famulus tarsus III	spine	spiniform seta	basal spine
famulus tibia I	*tibial organ	-	microseta

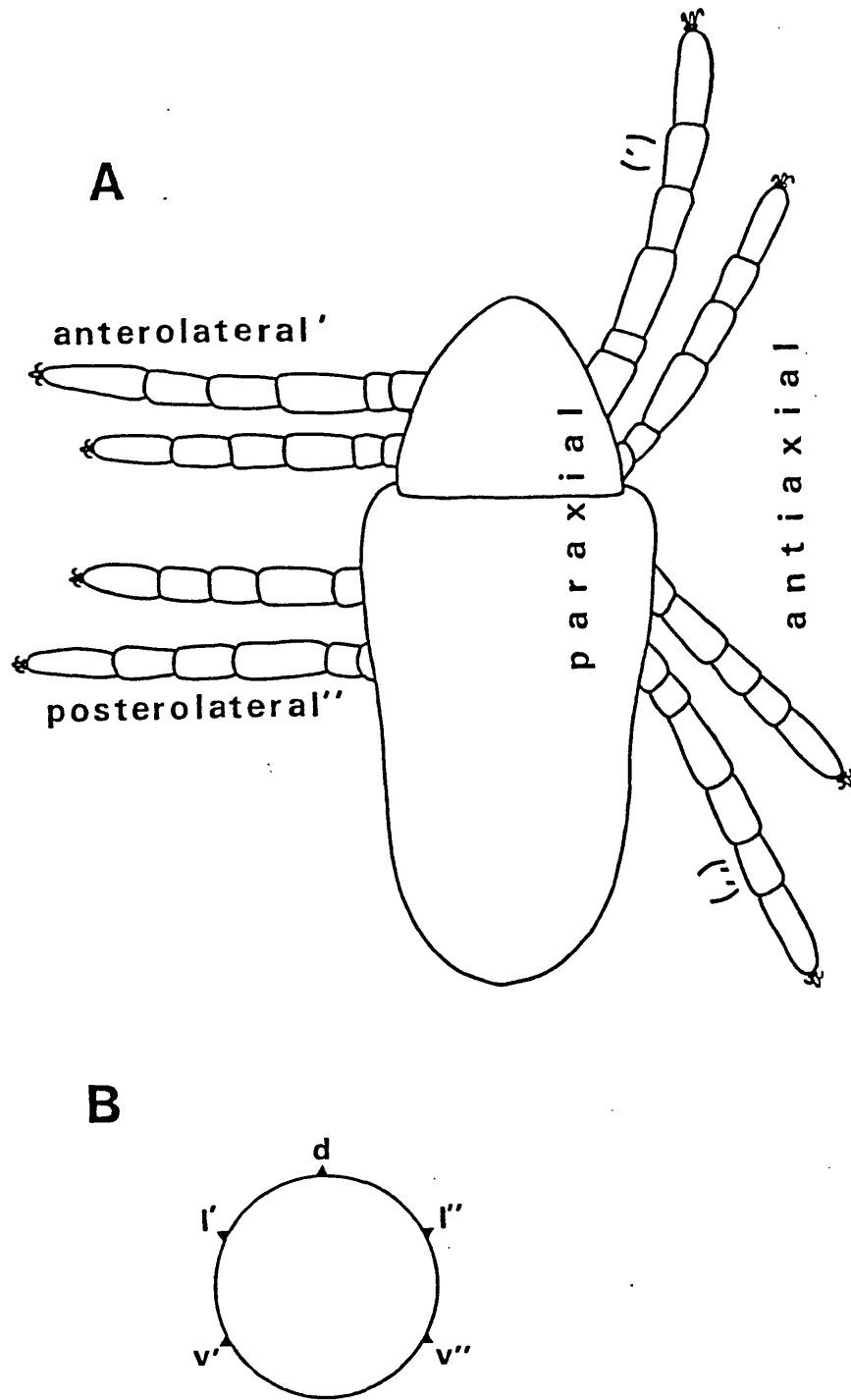


Fig. 6. Illustration of positional terms:

(A) The idiosoma and appendages; (B) Cross section through a leg segment showing a verticil of five setae.

7.3.2 General appearance

Eupodoid mites are weakly to moderately sclerotized, small to large in size (170 to 2000 μ m long). In life, they are often colourful - pink, red, black, green or combinations of these - and decorated with spots or stripes. The body is generally somewhat elongate and dorso-ventrally flattened. The four pairs of legs are quite slender, clearly visible and are rarely less than half the body length. As noted above, the first two pairs of legs are directed anteriorly and the last two posteriorly. Both the body and appendages bear setae of variable form.

7.3.3 Divisions of the body

Nomenclature of the body divisions referred to in this account is largely taken from Grandjean (1969) and is shown in Fig. 7. The most anterior part is the gnathosoma, comprising the subcapitulum, a pair of palps and a pair of chelicerae. The gnathosoma is carried subterminally but is visible from above and articulates with the main body, the idiosoma. The idiosoma is subdivided by a transverse furrow, the sejugal furrow, which encircles the body between the second and third pair of legs. In most genera, this furrow clearly divides the idiosoma dorsally into the anterior prodorsum (= aspidosoma of Grandjean (1969)) and the posterior opisthosoma. Ventrally, the area occupied by the four pairs of leg coxae is termed the podosoma, while the genital area and anal region are found on the ventral aspect of the opisthosoma.

7.3.4 The integument and associated structures

Ornamentation of the integument

The integument is lightly to moderately sclerotized; an account of the ultrastructure is given by Alberti et al (1981). Most commonly, it is decorated with fine spicules, papillae and/or striae (Figs 14a-d), although in some taxa, the ornamentation is reticulate (Fig. 14e). On the prodorsum (see following section for explanation of terms), the ornamentation of the naso sometimes differs markedly from that of the rest of the prodorsal integument (Figs 15b, d, e, 20e). In most genera, there is also an area of differentiated integument on the prodorsum forming a shield (Figs 14a, b, d). This shield usually lacks striae or possesses less densely spiculed striae.

The dorsal section of the sejugal furrow varies. It can be deeply invaginated (Figs 7, 17a) or be represented by a narrow transverse band of striae delimiting the prodorsum and opisthosoma but not clearly subdividing the idiosoma (Fig. 70). Where the sejugal furrow extends ventrally between coxae II and III, it is represented by a narrow band of transverse striae. Other dorsal furrows occur uniquely in the genus *Caleupodes* which exhibits external signs of primary opisthosomal segmentation (Fig. 17a, see also section 11). The limits of the segments are represented by slight furrows of differentiated integument (Fig. 14e).

Coxal integument is normally spiculate and/or papillate and lacks striae (Fig. 14f). The integument over the rest of the venter is usually similar to that of the dorsum whereas the integument of the genital shields and anal flaps is orientated in a different plane so that it appears to be somewhat differentiated (Figs 24b, 25).

The integument of the subcapitulum, palps, shaft and most of the fixed digit of the chelicerae is normally papillate or spiculate (Figs 22, 23a-e),

with only vestiges of striae or reticulations. The movable cheliceral digit and distal part of the fixed digit are smooth (Figs 22f, 23b, c, e), as are the ventral and dorsal faces of, respectively, the chelicerae and subcapitulum. The surface of the latter is channelled (Fig. 17c) where the two surfaces move against one another during feeding.

Finally, the legs usually lack striae, being papillate, spiculate or reticulate (Figs 17b, 26).

Setiform structures (Grandjean 1941a, 1947a)

Normal or true setae (Fig. 8A).

These are the most numerous type and occur on the idiosoma and appendages where they function as mechanoreceptors. They articulate with the integument *via* a membranous socket; a sensory neurone is associated with the base of the seta but its dendrites do not enter the shaft. The seta itself is composed of a central core of birefringent, anisotropic actinopilin which 'glows' in plane-polarized light (illustrated in rhagidiids by Ehrnsberger (1974)). External to the axis is a non-refractive isotropic layer and it is from the development of this that setal ornamentations arise. In the Eupodoidea, these range from weak serrations to dense feathering (Fig. 16).

Eupathids (Fig. 8B).

These are modified normal setae located on the tarsi of the legs and palps. The core of actinopilin is hollowed out and the lumen penetrated by the dendrites of the associated sensory cell. Eupathids are thought to correspond to the 'terminal pore sensilli' of insects (Altner & Prillinger 1980) and to be contact chemosensors.

Famuli (Figs 8D, F).

A famulus is similar to a eupathid internally, but is often much smaller or differently shaped. In eupodooids, they generally occur on tarsus I and II and often on tibia I.

The tarsal famuli are typically small and associated with a solenidion. On tarsus I, it comprises a short stalk and a globular centre-piece surrounded by a number of finger-like processes (Figs 8D, 17f). Rarely, the stalk is much elongated (Fig. 17d) or the processes are elaborately branched (Fig. 17e). On tarsus II, the famulus is in the form of a small spine (Figs 8F, 18a), while rarely it is elaborately branched (Fig. 18d).

The famulus of tibia I is located distally on the segment and is usually associated with a solenidion. It resembles a much reduced famulus of tarsus I, comprising a short stalk topped with a small 'dome' surrounded by a number of smaller papillae (Figs 18b, c).

Trichobothria.

These have a solid core of actinopilin and are inserted in distinct cavities, or bothridia.

In the Eupodoidea, there are two pairs of prodorsal trichobothria; the anterior internal vertical setae and the median pair (*T*). The interior of the bothridia is variously ornamented (Figs 14b, 20). Normally, the internal verticals are simple (Figs 15c, d, 20e) and the median trichobothria filiform (Figs 14b, 17a) but, in certain taxa, they are subclavate to capitate (Figs 20a, f). Opisthosomal seta (*f*₁) is sometimes similar in form to (*T*).

Trichobothria are regarded as vibroreceptors, although Beklemishev (1969), studying oribatid mites, suggests they are organs of balance.

Solenidia (Figs 8C, E).

These are hollow, thin-walled structures that are distinguished from other setae by the absence of actinopilin. They are found on the genu, tibia and tarsus of the legs and tibiotarsus of the palps, but, in most species, they are confined to the two distal segments of legs I and II. They are always smooth and are blunt distally. The alveolus is larger than in seta of comparable size.

In the Eupodoidea, the solenidia are of two types. That found in all taxa (the presence of which is one of the defining characters of the superfamily) is recumbent in a pit (Fig. 8C) although, in certain taxa, it is semi-erect (Fig. 19a). These are termed rhagidial organs and vary in form and size. Some, for example, are simply recumbent and L-shaped (Figs 18a, 19d), while others have a stalk and are T-shaped (Fig. 18e), have two attachment points and appear bridge-like (Fig. 59C), are U-shaped (Fig. 17e) or are very small (Figs 18f, g, 19c). Under the scanning electron microscope, rhagidial organs appear to be ridged (Figs 18a, b, d, e, 19b, d) and it is here suggested that they may be homologous with the 'sensilli with wall pores' of Altner & Prillinger (1980). The dendrites of the neurone associated with these sensilli extend into the lumen and branch outwards to terminate in longitudinal rows of small pores in the wall. They are considered by Altner & Prillinger to have a chemosensory function.

The second type of solenidion is similar to the usual acarine form, *i.e.* more or less erect (Figs 8E, 19e).

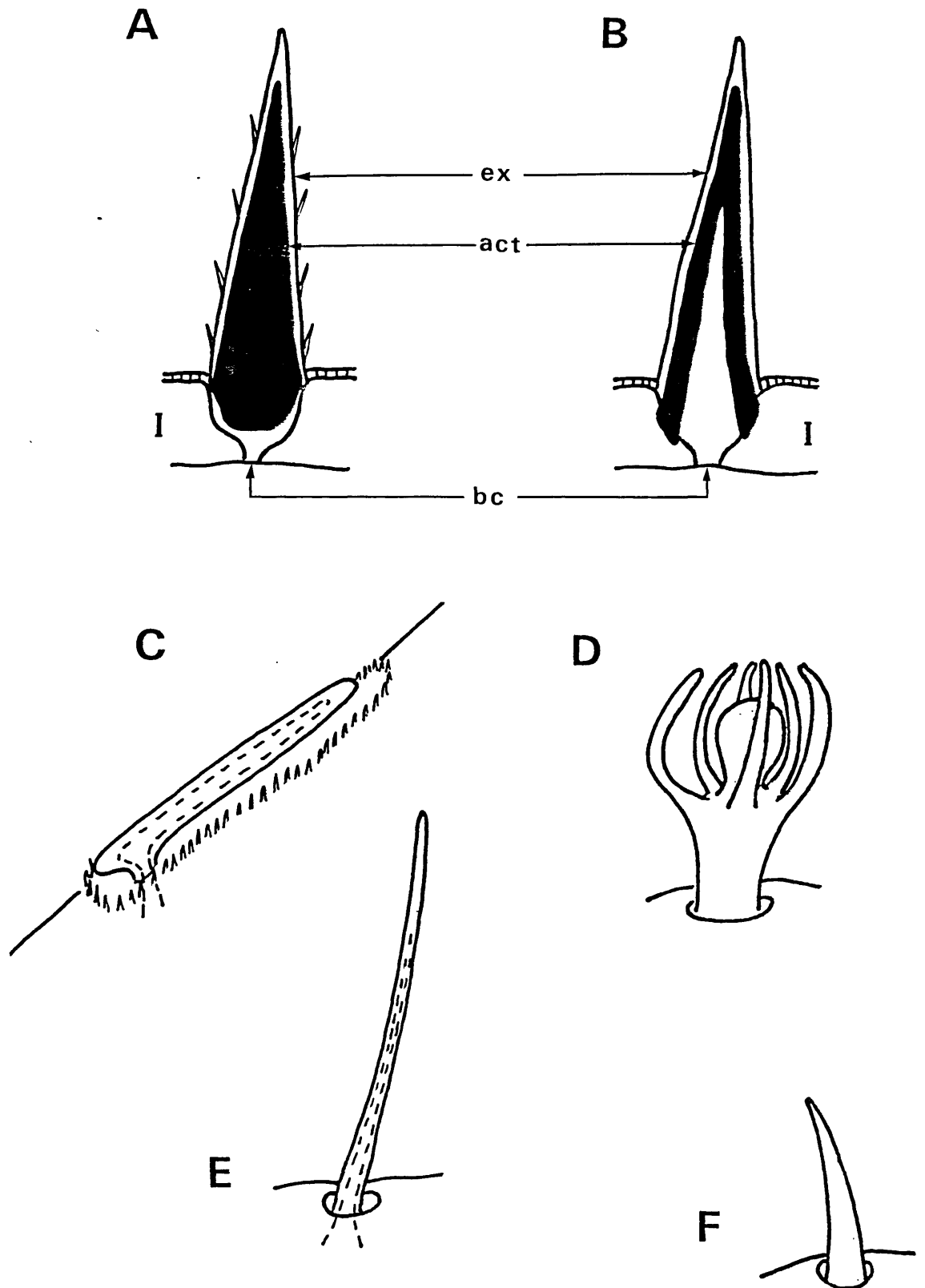


Fig. 8. Setiform structures:

(A) normal seta; (B) eupathid; (C) rhagidial organ - recumbent solenidion;

(D) famulus, tarsus I; (E) erect solenidion; (F) famulus, tarsus II.

act = actinopilin core, bc = basal cavity, ex = external isotropic layer, I = integument.

Lyrifissures.

Four pairs of lyrifissures occur on the opisthosoma. Although under the scanning electron microscope they do vary somewhat between taxa (Fig. 21), when viewed under the light microscope they mostly appear circular to elliptical in surface view (Fig. 9F), while in lateral aspect they are cup-shaped with a perforated base (Fig. 9G). In the family Penthalodidae, however, the lyrifissures are slit-like with a sclerotized margin, although this is not discernable in scanning electron micrographs (Fig. 21e).

Eyes.

When present, one pair occurs on the prodorsum. In the family Penthalodidae, the eyes are clearly visible raised circular areas of differentiated integument (Fig. 15e). In the other members of the superfamily, there is no superficial evidence of eyes but, in certain specimens, two pigmented areas with a granular appearance are sometimes evident (Fig. 7B).

7.3.5 Gnathosoma (Fig. 9)

The main skeletal structure of the gnathosoma is formed from extensions of the palp coxae. Dorsal and ventral extensions form a sclerotized tube, the gnathosomatic base, which partially encloses the bases of the chelicerae dorsally. The mesial walls of the palp coxae are connected horizontally by the subcheliceral plate which divides the gnathosomatic cavity into the dorsal cheliceral region and the anterior subcapitular region.

Subcapitulum (Fig. 9A,B)

The subcapitulum is the roughly cone-shaped part of the gnathosoma, formed from distiventral extensions of the palp coxae, which occurs anteriorly to the gnathosomatic base. Ventrally, there is a median fissure extending along the distal half of the subcapitulum dividing it into two lateral lips, the apices of which are sometimes further subdivided into the internal mala and external mala. Between the lateral lips, a pointed structure can often be observed. This is the distal part of the labrum which covers the preoral cavity dorsally (Fig. 15f).

There are always two pairs of subcapitular setae. One pair (sbc_1) is located laterally at the base of the subcapitulum, while (sbc_2) is inserted ventrally, its position varying from subapical to level with (sbc_1). Two, or rarely one, pairs of smooth, eupathidial adoral setae (or_1 & 2) occur apically. In the families Eupodidae, Penthaleidae and Penthaleodidae the adoral setae are minute and often difficult to discern under the light microscope (Figs 22c, e). In the Rhagidiidae, however, these setae are much longer and clearly visible (Fig. 22b) but, rarely, only (or_2) is present.

As noted above, the dorsal face of the subcapitulum is grooved to accommodate the protraction and retraction of the chelicerae (Fig. 17c).

Chelicerae (Figs 9C,D,E)

Grandjean (1947a) considered the primitive acarine chelicera to consist of segments like those of the other appendages. Thus the small basal part of the main shaft is homologous with the trochanter, while the remainder is a compound segment formed by the fusion of the femur, genu, tibia and tarsus. The movable digit of the chela is thought to be homologous with the apotele

of a walking appendage and the fixed digit derived from up to four birefringent setae on the penultimate segment.

In the Eupodoidea, the paired independent chelicerae account for about one fifth of body length. The main shaft, forming the bulk of the appendage, terminates in a subchelate to strongly chelate portion. The fixed digit can be simple and slightly forked (Figs 9C, 22f), terminate in finger-like processes (Fig. 9D) or be strongly hooked (Figs 9E, 23b), while the movable digit is weakly or strongly hooked (Figs 22f, 23b, e). In certain taxa, the chela are much reduced (Fig. 23c). The chelate part accounts for about one tenth to one half of the total cheliceral length.

One or two cheliceral setae occur although, rarely, the chelicerae are devoid of setae. When present, the proximal seta (*cha*) is located dorsally or slightly antiaxially, just proximal to or on the fixed digit, while the distal seta (*chb*) is located antiaxially on the distal part of the fixed digit.

Fig. 9. External morphology, gnathosoma & lyrifissures:

(A) *Eupodes abbreviatus* n.sp., subcapitulum, venter;

(B) *Rhagidia clavicrinita*, apex of subcapitulum, venter;

(C)-(F) chelicerae, *E. abbreviatus* (C), *Penthalodes ovalis* (D),

Penthaleus longipilis, chela (E), *Rhagidia punkva* (F);

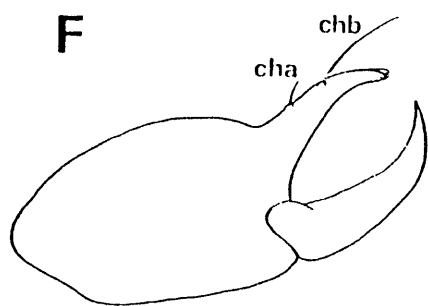
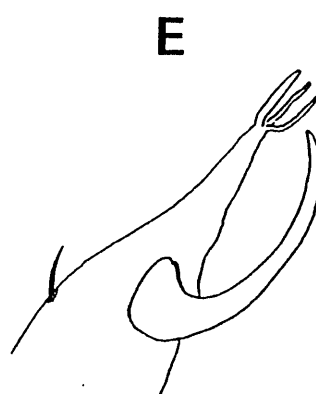
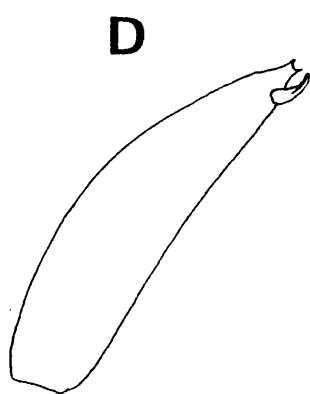
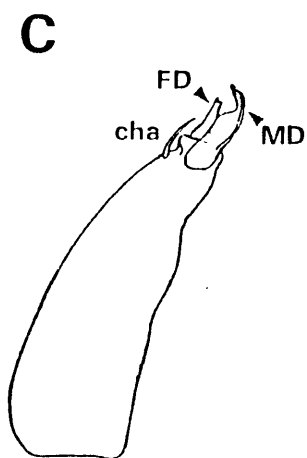
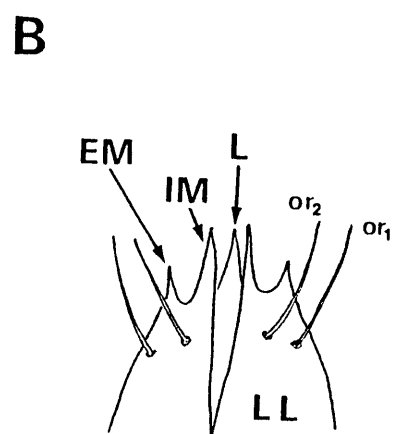
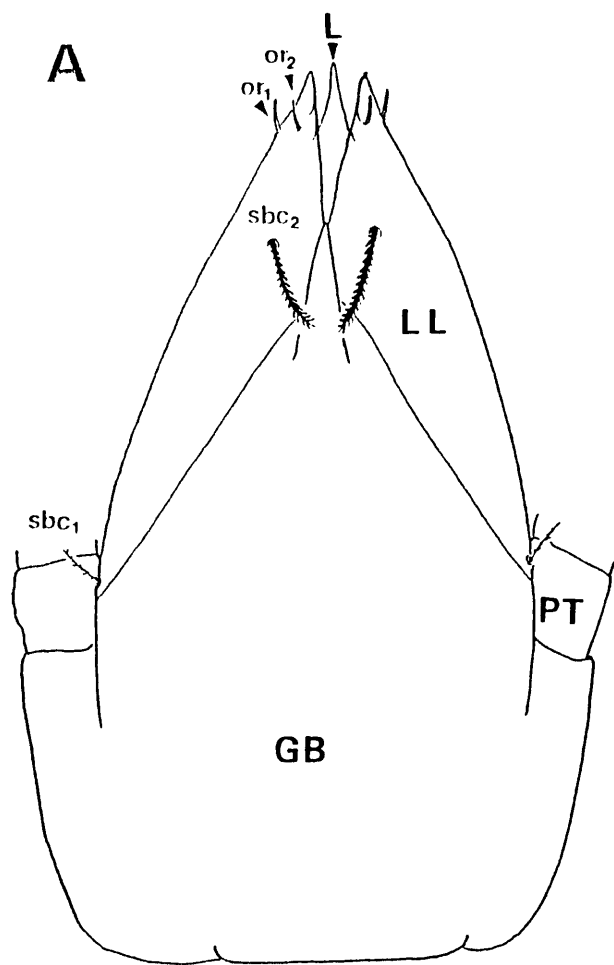
(G)-(H) lyrifissure, surface (G), lateral (H).

EM = external mala, FD = fixed digit, GB = gnathosomatic base,

IM = internal mala, L = labrum, LL = lateral lip, MD = movable

digit, or = adoral seta, PT = palp trochanter, sbc = subcapitular

seta.



Palps (Figs 10A-C)

The palps are simple and divided into four segments - the trochanter, femur, genu and tibiotalrus. The coxae, as noted above, are expanded and fused to form the basic skeleton of the gnathosoma. They are normally long and slender, extending past the apex of the subcapitulum, but in the family Penthaleidae they are short and robust.

The coxa has a small, variously ornamented supracoxal seta (*e*) located dorsodistally (Figs 23f, g) (Grandjean 1936). The femur and genu have respectively two (*d*₁, *d*₂) and three setae (*d*, *l*'*l*""). The tarsus most commonly supports nine or 10 setae, although in the Rhagidiidae other complements occur. Normally, an antiaxial rhagidial organ or a dorsal erect spiniform solenidion (*ω*) occurs on the tibiotalrus.

Based on Grandjean (1935a), the tibiotalrusal setae are named as follows (Fig. 10A): a dorsal seta (*d*), flanked by two lateral setae (*l*'*l*""), an unpaired posterolateral seta (*sl*""), a dorsal, subterminal anteroculminal seta (*acm*), a pair of terminal prorals (*p*'*p*""), a terminal or subterminal ventral seta (*v*) and a ventral seta (*ba*). When ten setae are present, *v* is paired.

7.3.6 Idiosoma - dorsum (Fig. 7B)

Prodorsum

The anterior of the prodorsum is produced into the naso. This varies in its development, for example, it can be a slight extension of the prodorsum (Fig. 15c), a clear peak (Fig. 20f) or a delimited lobe (Figs 20e, 15b, d) or dome (Fig. 15e). In the family Penthaleidae, a tri-lobed structure, the epirostrum, is associated with the naso (Fig. 10D). It extends anteriorly, partly covering the dorsum of the gnathosoma.

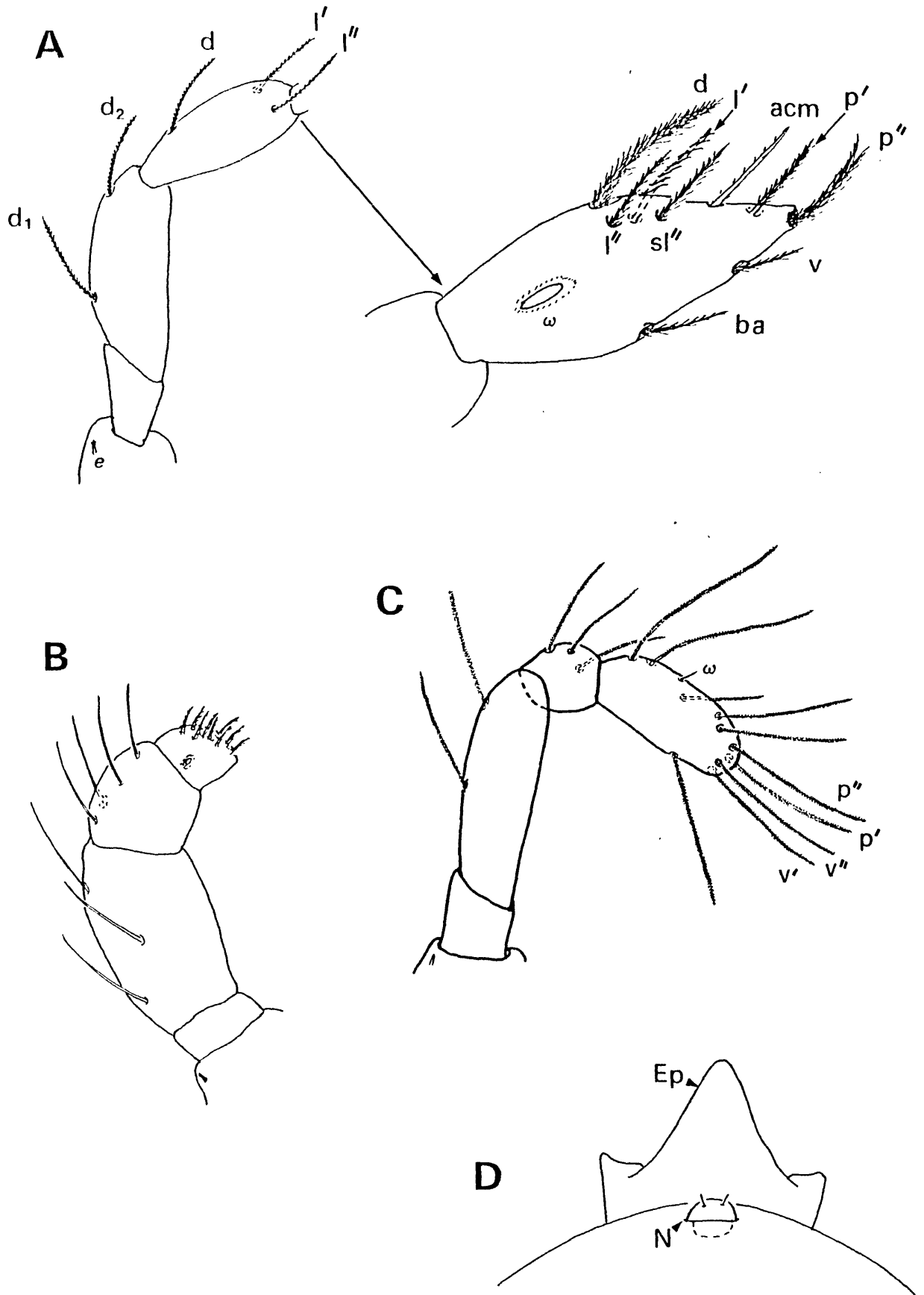


Fig. 10. External morphology, palps & epirostrum:

(A)-(C) palpal form, antiaxial aspect, (A) *Eupodes abbreviatus*, with tibiotarsus enlarged, (B) *Fenthaleus minor*, (C) *Rhagidia punkva*; (D) *Fenthalodes ovalis*, epirostrum & naso.

Ep = epirostrum, N = naso, e = supracoxal seta.

The prodorsum normally supports four pairs of setae, arranged more or less as in Fig. 7B. The most anterior pair, the internal vertical setae (*iv*), are situated on, at the base of or just posterior to the epivertex (Figs 20e, f). The external vertical setae (*ev*) are found either just lateral to the trichobothria (*T*) or some way between them and (*iv*). The fourth setal pair, the scapular setae (*sc*), are located slightly anteriorly or posteriorly to (*T*).

In the genus *Pilorhagidia*, a fifth pair of prodorsal setae is located between (*T*) and (*ev*).

Opisthosoma

The opisthosoma normally bears eight pairs of setae and three pairs of lyrifissures.

The setae are arranged in pairs in five horizontal rows, each corresponding to an opisthosomal segment (Figs 7A, B). This is most clearly demonstrated in the genus *Calepodes*, where the segments are partially delimited (Figs 7A, 14e, 17a. See also section 11). From anterior to posterior they are denoted C, D, E, F and H and their setae are respectively (*c*₁) and (*c*₂), (*d*₁), (*e*₁), (*f*₁) and (*f*₂), (*h*₁) and (*h*₂) (Grandjean 1947). When hypotrachy occurs, (*f*₁) or the (*h*) row is absent. In certain of the genera where the sejugal furrow is indistinct, the lateral margins of opisthosomal segment C extend around the prodorsum so that opisthosomal setae (*c*₁) are level with (*T*) (Fig. 70). As noted above, opisthosomal trichobothria sometimes occur in the (*f*₁) position.

One pair of lyrifissures occurs lateral to the setae on segments D, E and F (Figs 7A, B). These are respectively denoted (*ia*), (*im*) and (*ip*).

7.3.7 Idiosoma - venter (Fig. 7C)

Podosoma

The leg coxae are fused to the ventral body wall (sometimes termed a coxisternum), with only a small distal portion free. In cleared specimens, their limits can be seen as variously sclerotized epimeres. Those of the families Eupodidae and Penthaleidae are faintly but clearly delimited, although the proximal edges are sometimes indistinct. In the Penthaleodidae, only the distal limits are delimited, but heavily so. In the Rhagidiidae, the coxae are, for the most part, clearly and completely defined. The respective pairs of coxae do not fuse proximally but, on either side of the body, coxae I and II and coxae III and IV are contiguous, while coxae II and III are quite widely separated by the sejugal furrow. The coxae thus form four groups, each comprising two coxae.

A distal, anterolateral supracoxal seta occurs on coxa I (*eD*) which is of the same form as that found on the respective palp coxa (Figs 23f, g). A number of setae are inserted on the ventral face of the coxae, some are located within the limits of the coxae, while others, in cleared specimens, appear to be just outside. In scanning electron micrographs, however, the latter are usually seen to be inserted on the typical coxal integument. The setal nomenclature is based on the system devised by Grandjean (1935b). Coxae I and II possess, respectively, three (*1a,b,c*) and one (*2b*) setae, III has from three to seven (*3a,b,c-g*), while IV has two or three (*4a & b* or *4a,b-c*) setae.

Genital area (Fig. 11)

The genitalia are located approximately centrally on the opisthosoma. The genital aperture is surrounded by a variable number of eugenital setae (setal terminology taken from Grandjean 1949) which, in females, are usually mounted on papillae and are longer and more widely spaced than in males. Lateral to the eugenital setae are two pairs of genital papillae which comprise a cylindrical base topped with a dome (Fig. 24d). This genital chamber is covered with a pair of, usually, roughly kidney-shaped genital shields, that are generally longer in the female than in the male. In the family Penthalodidae, the shields are rounded rectangular and clearly delimited from the surrounding integument (Fig. 24C). The shields support a variable number of genital setae which are arranged in single file near the free margin (Fig. 24b) or with one or more located laterally to these (Fig. 11A). Bracketing the genital shields are a number of pairs of aggenital setae.

The female ovipositor is either a simple evagination of the membrane surrounding the genital aperture and genital papillae or is a well-developed extrusible tube encircled by the eugenital setae (Fig. 11C).

In macerated specimens, the male can be seen to have a number of sacs leading into the genital aperture (Fig. 11B). The largest of these, the sperm sac, is subclavate to capitate and either unornamented or clearly ornamented with a reticulate patterning. The other, accessory glands, are smaller and never ornamented.

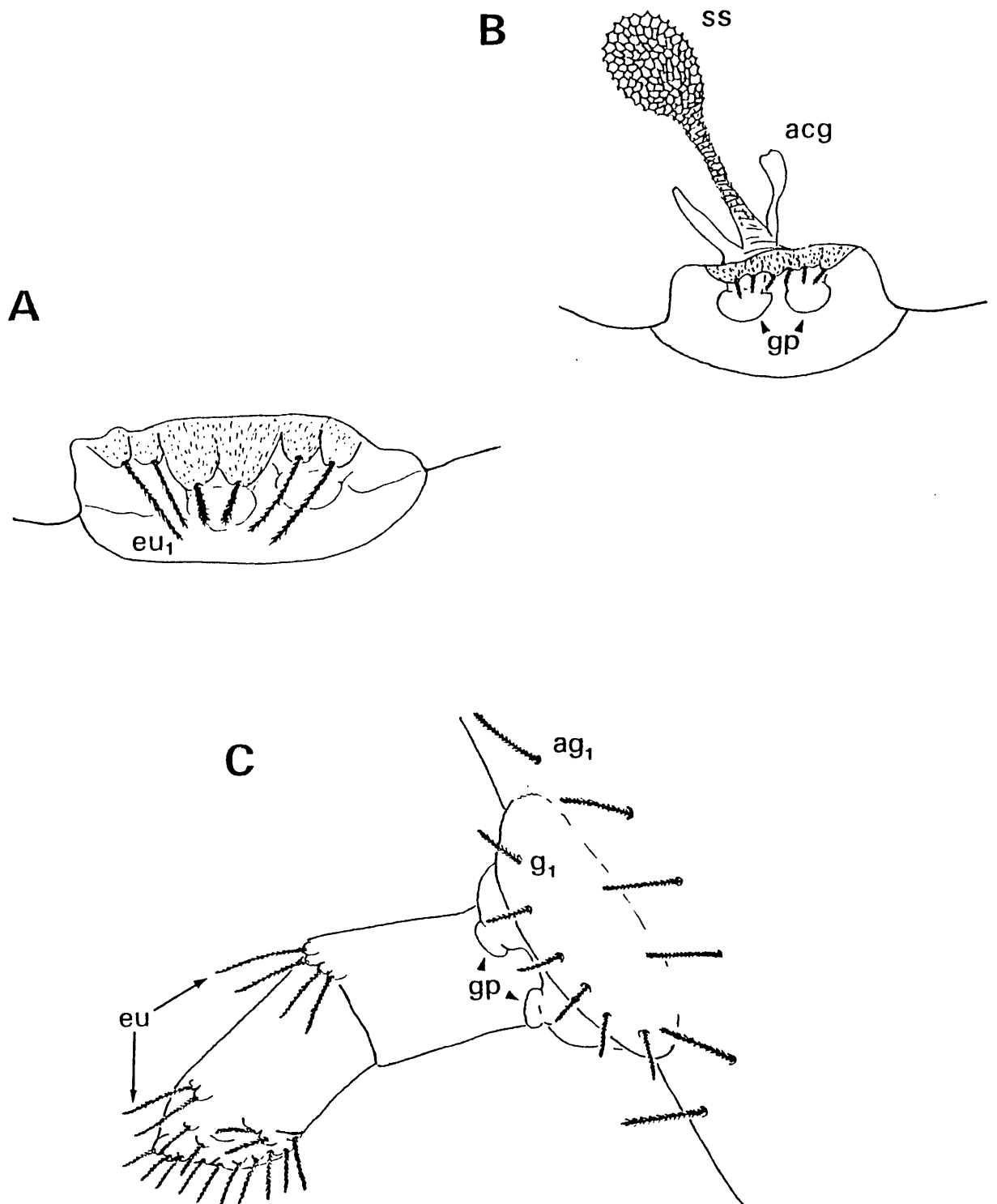


Fig. 11. External morphology, genital area:

(A) *Eupodes alaskanensis* ♀, sagittal section;

(B) *E. alaskanensis* ♂, sagittal section;

(C) *Rhagidia clavicornita*, ovipositor.

acg = accessory gland, ag = aggenital seta, eu = eugenital setae, g = genital seta, gp = genital papillae, ss = sperm sac.

Anal region

The anus opens onto the last opisthosomal segment, the adanal. The opening is located dorsally, terminally or subterminally. It is normally slit-like and bordered by two flaps (Fig. 25), although in the genus *Penthaleus*, the anus is dorsal and opens *via* a short tube (Fig. 24a).

Apart from in members of the Rhagidiidae, the anal flaps are devoid of setae, the most posterior being the two or three pairs situated on the penultimate segment, the pseudanal. These are named, from dorsal to ventral, (ps_{1-3}) (Figs 7C, 25d). When only two pairs are present, (ps_2) is absent (Fig. 25a). In the Rhagidiidae, three pairs of pseudanal setae are present while one pair of adanals (ad_1) is located on the differentiated integument of the anal flaps (Fig. 25b).

A pair of lyrifissures (lh) is present on segment H, just lateral and anterior to (ps_3) and are of similar form to the dorsal lyrifissures (Fig. 21).

7.3.8 Legs

The legs comprise seven free segments, joined by arthrodial membranes. From proximal to distal the segments are the trochanter, femur, genu, tibia, tarsus and apotele (= ambulacrum). The femur is usually subdivided to a greater or lesser extent but, since both parts always share musculature, they do not form separate segments. For ease of reference, however, the terms basi- and telofemur will be utilized for the two parts. The basifemur is sometimes greatly enlarged (Fig. 49F).

Articulations

It has just been noted that the leg segments are joined by arthrodial membranes, but other structures also control their movement. Between the

trochanter and femur, there is a dicondylic mechanism which facilitates promotor-remotor movements (Manton 1977), allowing the legs to swing during walking. Dorsally, this mechanism comprises a dorsal trochanteral spine which fits into a femoral cavity (Figs 26a, b), while ventrally there is a much reduced arrangement (Fig. 26d). The articulation between the other segments is apparently monocondylic, comprising a rounded condyle on the proximal segment which fits into an acetabulum on the distal (Fig. 26c). This allows lateral movement as well as simple flexor-extensor movements.

In genera with enlarged femora IV, the articulation between the two subdivisions comprises a narrow strip of smooth integument flanked by papillae (Fig. 26e). Where subdivision is least marked, it is indicated by a ventral crease in the integument (Fig. 26f).

Apotele

The apotele is a free segment. It comprises a basal sclerite, representing the much reduced body of the segment and a pair of claws flanking an empodium, both of which are specialized setae (Grandjean 1941). Muscles originating in the tarsus permit movement.

In the Eupodoidea, the claws are hooked and rayed while the empodium is expanded and pad-like with ventral rows of thin filaments (Fig. 27). The apotele is occasionally reduced (Fig. 27d) or greatly enlarged and elaborate (Fig. 125A,C).

Setiform structures

The work of Grandjean demonstrated that acarine setiform organs form organized patterns, or taxies (see Norton 1977 for review). In the Eupodoidea, setal complements vary between species and between most genera

(see section 10 for details). Despite this variability in numbers, certain setal patterns can be discerned which permit Grandjean's notation systems for leg chaetotaxy to be applied.

Grandjean (1940) proposed that, primitively, the legs consisted of numerous short annuli, each with a whorl of setae of some basic number. The leg segments and their chaetotaxies seen now are the result of fusion of these annuli and reduction in the number of setal whorls. In the Eupodoidea, the maximum number of setae in a whorl is five, comprising a dorsal seta, *d*, two laterals, *l',l''*, and two ventrals, *v',v''*, (Fig. 6b). The whorls, even incomplete ones, are generally easy to identify apart, that is, from on the tarsus which supports the greatest number, the maximum being 28. Grandjean's (1935b, 1940) special notation system for the tarsus assumes the basic number of 20 setae, some of the homologues of which can be identified in eupodoids as follows (Fig. 12). Two pairs of setae surround the base of the apotele, namely a dorsal pair of prorals (*p*) and a ventral pair of unguinals (*u*). The iteral setae (*it*), the tectals (*tc*), the solenidia, the famulus and then the fastigials (*ft*) are located posteriorly to the prorals. Ventrally, posteriorly to the unguinals, a variable number of usually paired ventral setae (*pv*) occur whose numbered suffix indicate the order of appearance. A maximum of two pairs of lateral setae, *pl', pl''* and *l', l''*, can be present, while another pair of dorsal setae (*pd*) sometimes occurs posteriorly to the fastigials.

Instead of forming whorls, the solenidia mostly occur in longitudinal rows. Genual solenidia have the notation sigma (σ), those of the tibia phi (ϕ) and those of the tarsus omega (ω). The subscripted numbers refer to the order in which the solenidia appear during ontogeny.

The famulus of the tarsi are denoted by epsilon (ϵ), that of tibia I by (*k*).

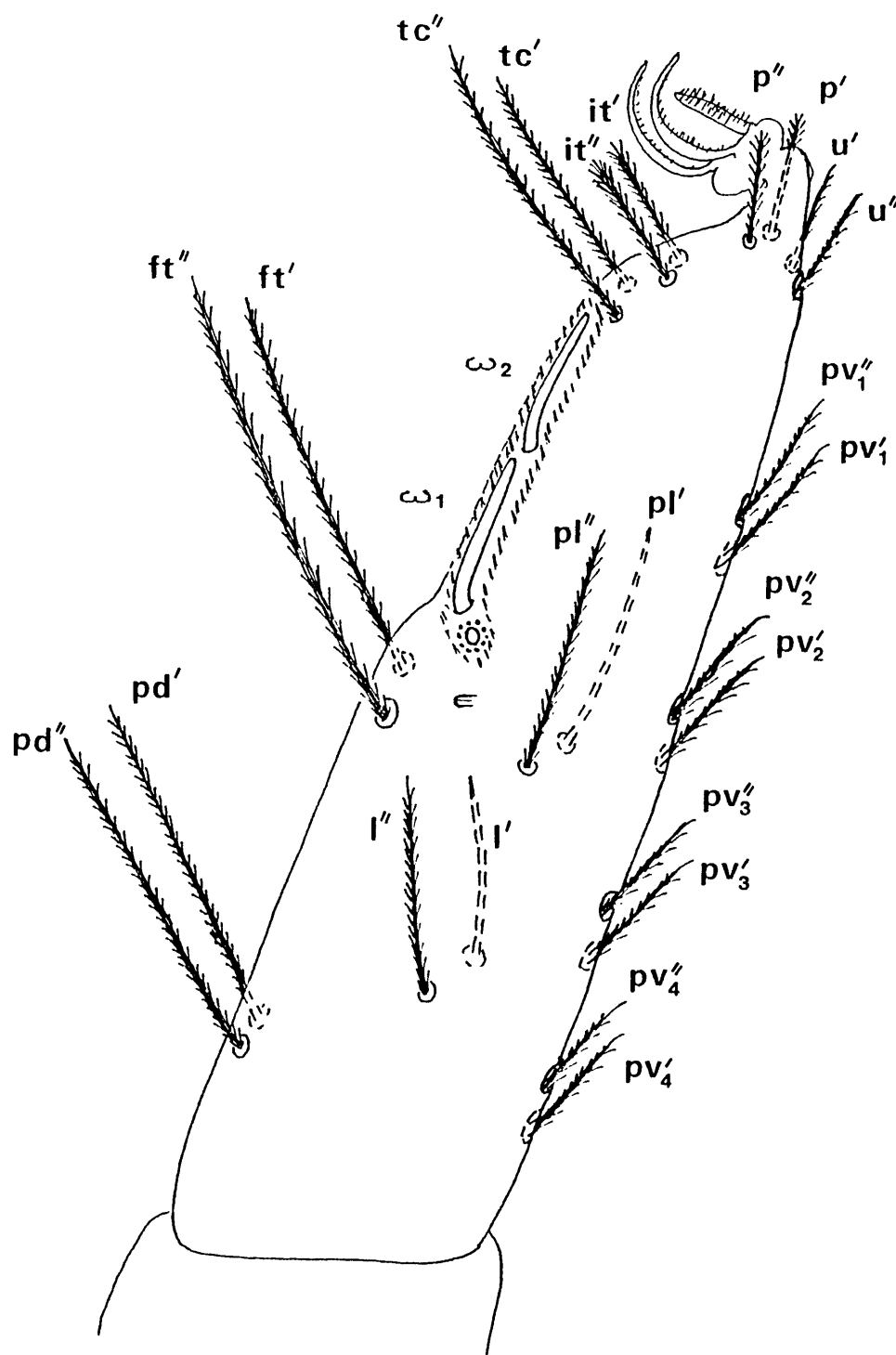


Fig. 12. Tarsal chaetotaxy: posterolateral aspect of generalized eupodid tarsus I.

7.3.9 Immature stages

Like other primitive prostigmatids, eupodoids show no reduction in the number of immature stages; that is, they have five from egg to adult. The first is an inactive prelarva, followed by an active larva and three active nymphs, the proto-, deuto- and tritonymphs. Due to the inactive habit of the prelarva, these were not extracted from soil samples by the methods used in this study and they have not been included in descriptions of taxa. Descriptions of eupodoid prelarvae can be found in studies by Coineau (1976) and Ehrnsberger (1974).

The active immature stages are all similar to the adult in general appearance and all have the full complement of hypostomal, cheliceral, dorsal idiosomal and pseudanal setae. However, the coxae and the free leg segments are deficient in setae and solenidia and these are added progressively at each stage. All immature stages lack eugenital and a certain number of genital papillae and genital and aggenital setae and it is by the state of the genital region that the immature stages can most readily be separated from each other. The following account (illustrated in Fig. 13) details the distinguishing features of each stage but, for a more detailed discussion of ontogenetic development, see Section 11.

Larva

As is the normal case in mites, larval eupodoids are hexapod, lacking leg IV. They are also devoid of any external signs of genitalia.

Like those of other taxa with genital papillae in nymphal and adult stages, eupodoid larvae possess a pair of Claparède organs between coxae I and II (Baker, A.S. 1985). Several authors have referred to the presence of these organs in eupodoid larvae (Ehrnsberger 1974, Grandjean 1945, 1946, Knülle 1959), but none provided descriptions or figures. Although

discernible under the light microscope, the use of the scanning electron microscope established the presence and revealed details of the external morphology of eupodoid Claparède organs. Some variation occurs, but it is evident that the same general form is present in all taxa. The Claparède organ comprises a cylindrical protuberance, rounded distally, with an associated cap originating from the base of the posterolateral free margin of coxa I (Figs 28a-e). The protuberance possesses a spiculed integument like that covering the coxae, while the apical dome is smooth (Figs 28b, d, e). As in other superfamilies, the Claparède organs resemble the genital papillae of the nymphs and adults (Fig. 28f). The shape and position of the cap are such that it can cover the smooth dome (Figs 28b, e).

According to Alberti (1979), this ability prevents water-loss. The under-surface of the cap is smooth (Fig. 28d) while, in larvae of examined species of *Cocceupodes* and *Eupodes*, the upper surface has a coxal-type integument (Figs 28d, e); in *Penthaleus*, by contrast, both surfaces are smooth (Fig. 28b). Another difference in the form of the cap occurs at its point of attachment. In species of *Cocceupodes* and *Eupodes*, it is broadly based (Fig. 29b), whereas in *Penthaleus*, it is stalk-like (Fig. 28b).

Although usually stored beneath the genital flaps (Fig. 24b), the genital papillae are sometimes extruded (Figs 24d, 28f), for example, during oviposition or, in terrestrial species, for the uptake of water (Alberti 1979). Extrusion is effected by hydrostatic pressure, while the papillae are retracted by the contraction of muscles attached to their base (Prasse 1970). There is some evidence that Claparède organs have a similar facility for movement as, in several specimens, they appear to be somewhat withdrawn (Figs 29a-c).

At this stage, there are six opisthosomal segments and the anal plates bear the pseudanal setae, with lyrifissure (*ih*) slightly anterior to the fissure delimiting the shields (Fig. 25c).

Protonymph

In addition to leg IV, the external genitalia appear at this stage and comprise one pair of genital papillae, covered by the genital shields, and one pair of genital setae, the aggenitals still being absent.

The pseudanal setae and (*ih*) are now clearly located on the integument surrounding the anal flaps.

Deutonymph

The genitalia comprise two pairs each of genital papillae, genital and aggenital setae.

Tritonymph

Three pairs of genital setae and usually three but sometimes four or five pairs of aggenitals are now present.

In some nymphal specimens, a prodorsal dehiscence line was observed (Fig. 29d), a feature also observed in tydeids (Thor 1933, Marshall 1970, André 1979), caeculids (Coineau 1974) and cunaxids (Den Heyer 1979).

Fig. 13. Life stages - distinguishing features in genital and anal regions:

Ad = adult (with right genital shield removed), ag = aggenital setae, an = anus, DN = deutonymph, eu = eugenital setae, g = genital setae, g.p. = genital papilla, g.sh = genital shield, ih = ventral lyrifissure, *ih*, L = larva, PN = protonymph, ps = pseudanal setae, TN = tritonymph.

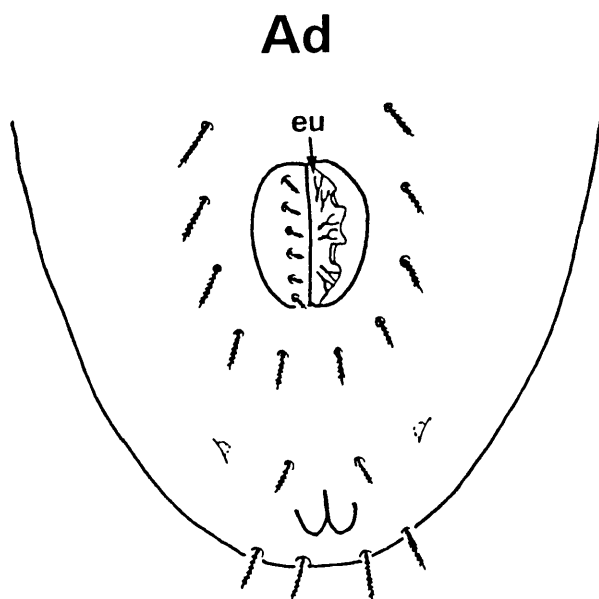
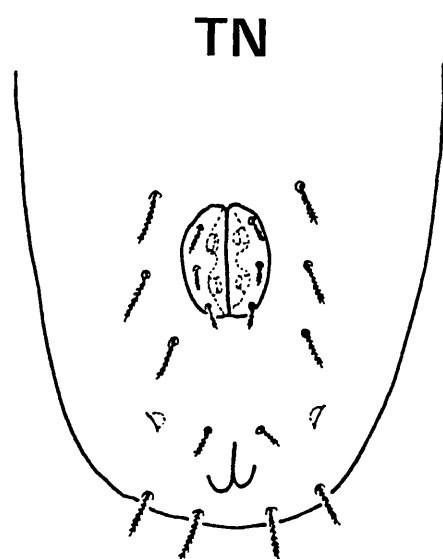
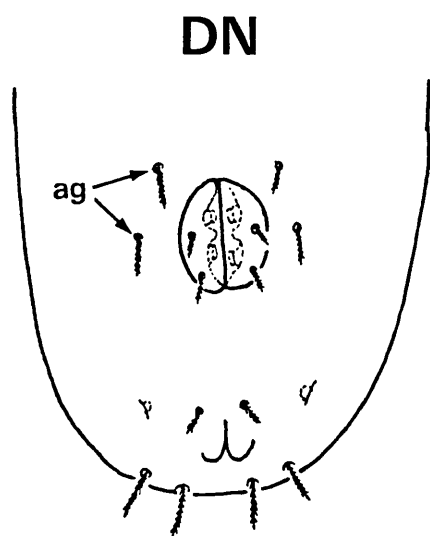
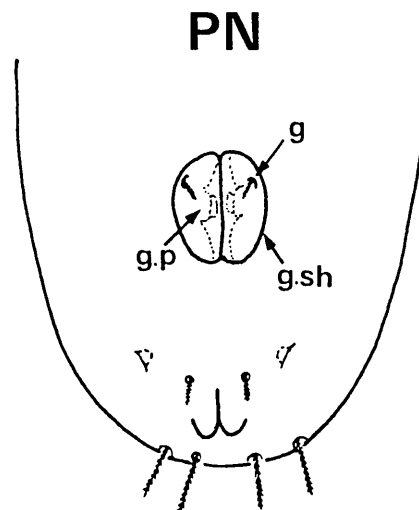
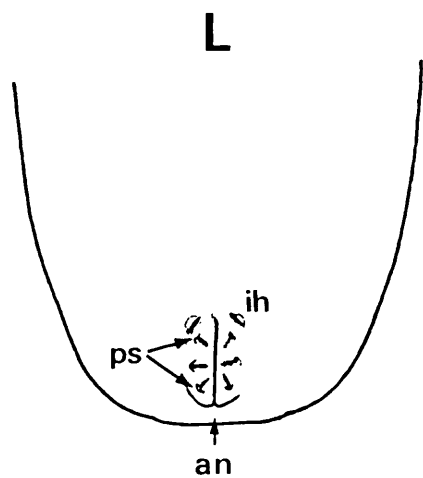


Fig. 14. Ornamentation of the integument:

- (a) *Eupodes alaskanensis*, view across margin of prodorsal shield (x13600).
- (b) *Alloeupodes interruptus*, margin of prodorsal shield arrowed (x1200).
- (c) *Penthalodes ovalis*, dorsum (x6280).
- (d) *A. interruptus*, view across margin of prodorsal shield (x11000).
- (e) *Caleupodes reticulatus*, opisthosomal furrow arrowed (x2700).
- (f) *Rhagidia* sp., coxal integument (x508).

co = coxa, ps = prodorsal shield, T = trichobothrium.

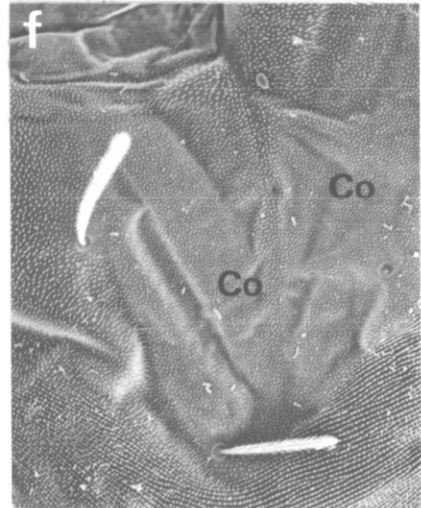
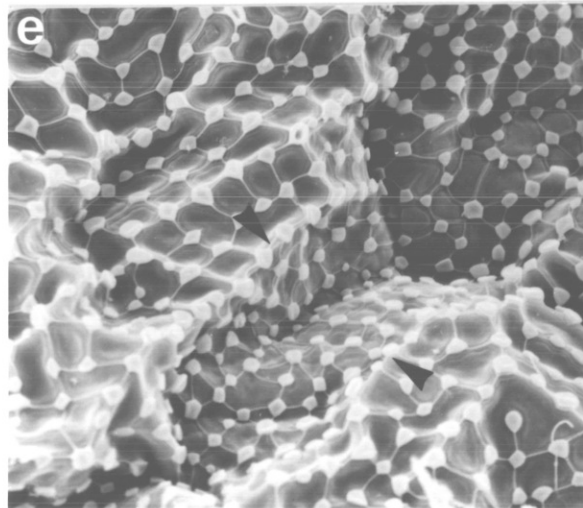
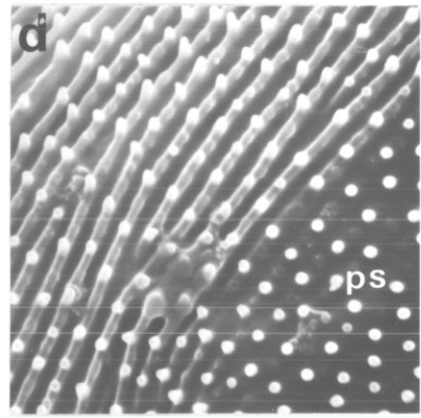
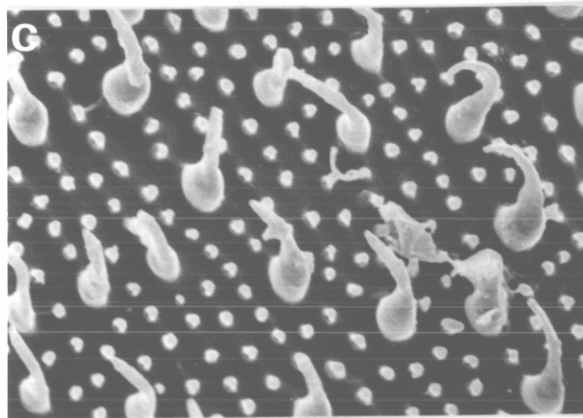
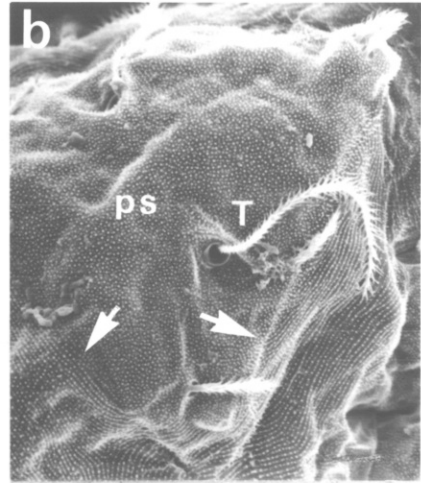
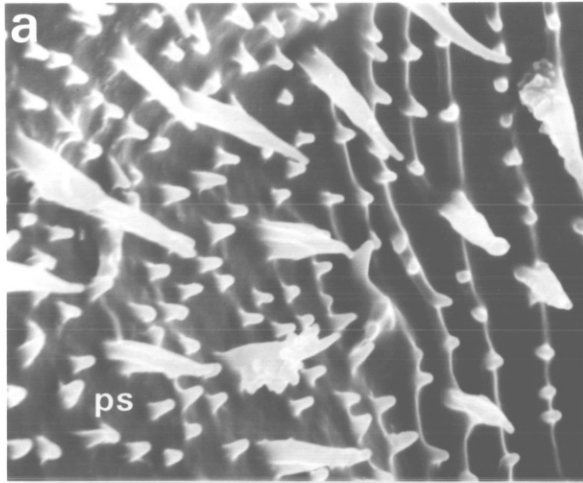


Fig. 15. Prodorsum and gnathosoma:

- (a) *Penthalodes ovalis*, raised prodorsal eyes (x1985).
- (b) *Rhagidia sp.*, naso (x1300).
- (c) *Coccorhagidia macrostella*, naso (x5000).
- (d) *Penthaleus minor*, naso (x658).
- (e) *P. ovalis*, naso (x2167).
- (f) *Cocceupodes breweri*, anterodorsal view of subcapitulum (x8519).

E = eye, ev = external vertical seta, N = naso,

iv = internal vertical seta, L = labrum, V = venter.

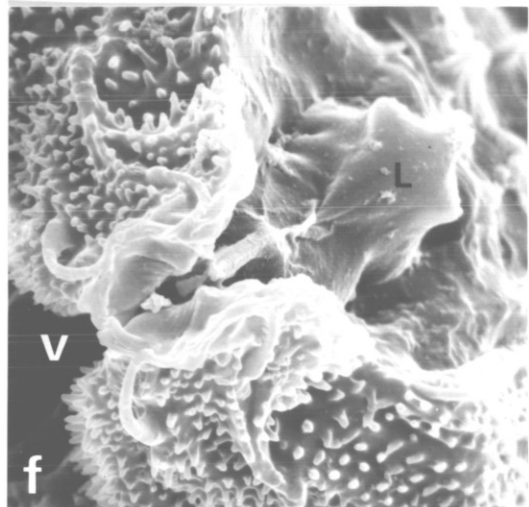
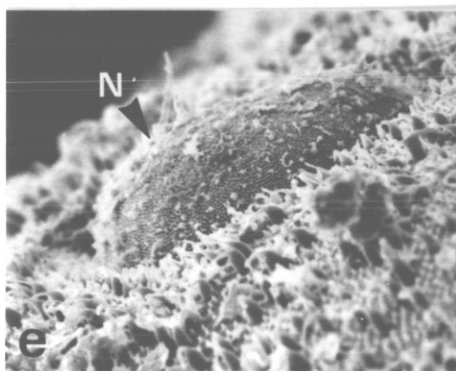
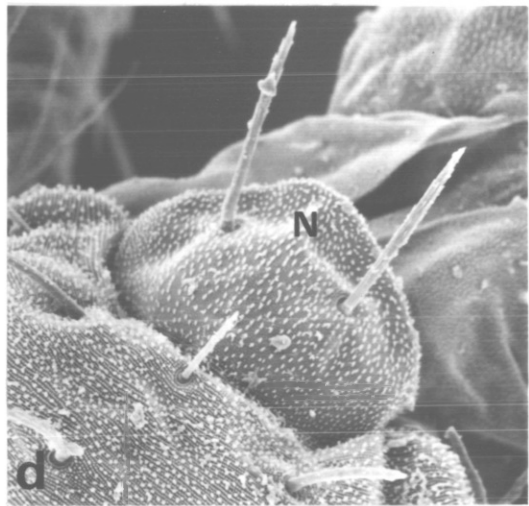
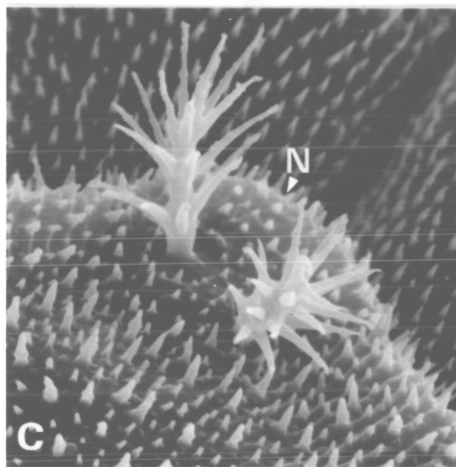
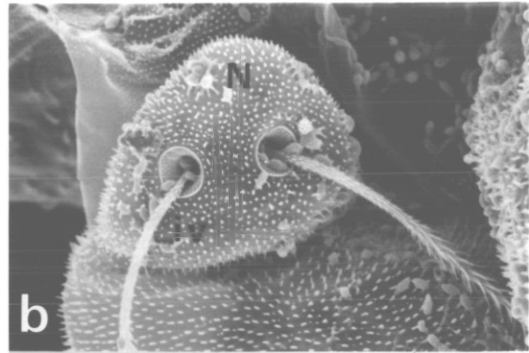
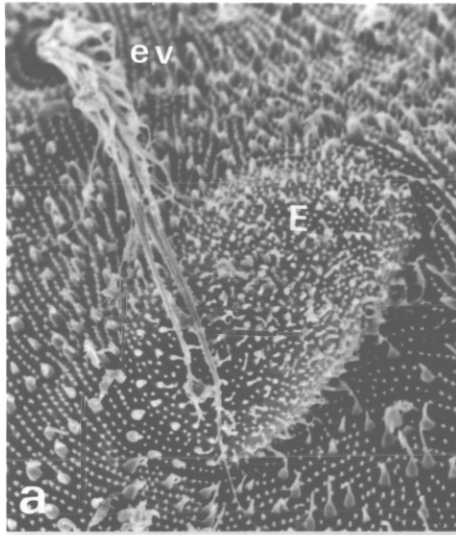


Fig. 16. Setal ornamentation:

- (a) *Penthaleus minor*, weakly serrate dorsal seta (x1800).
- (b) *Eupodes alaskanensis*, e_1 , densely spiculated (x1985).
- (c) *Cocceupodes trisetatus*, c_1 , spinose (x2500).
- (d) *Penthalodes ovalis*, f_1 , densely spinose terminating in long filament (x2300).

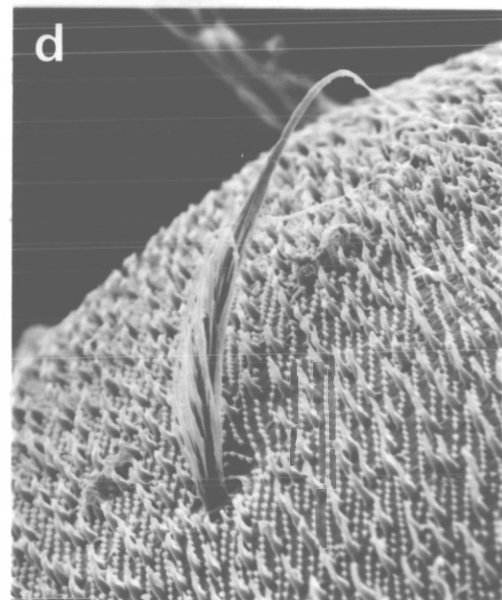
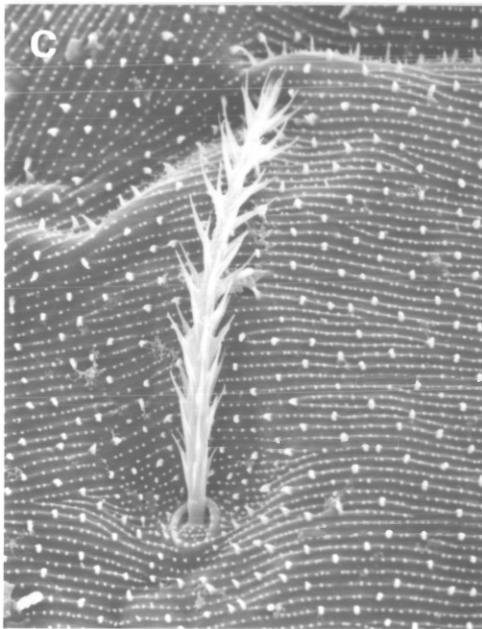
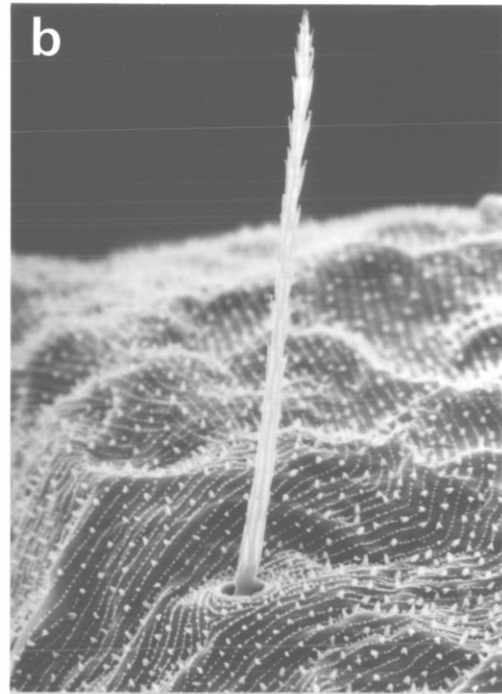
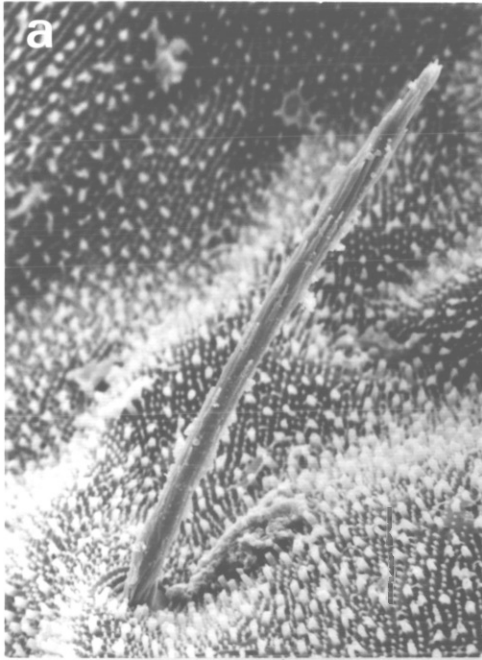


Fig. 17. Aspects of the integument and setiform structures:

- (a) *Caleupodes reticulatus*, dorsal view (x270).
- (b) *C. reticulatus*, leg integument (x10333).
- (c) *Cocceupodes breweri*, dorsal view of gnathosoma with chelicerae displaced. (x1350).
- (d) *Shibala heteropoda*, stalked famulus of tarsus I, location of globular structure arrowed (x5000).
- (e) *Coccorhagidia macrostella*, distal portion of tarsus I showing elaborate famulus and U-shaped rhagidial organ (x2542).
- (f) *C. reticulatus*, famulus tarsus I (x7368).

Ch = chelicera, S = subcapitulum.

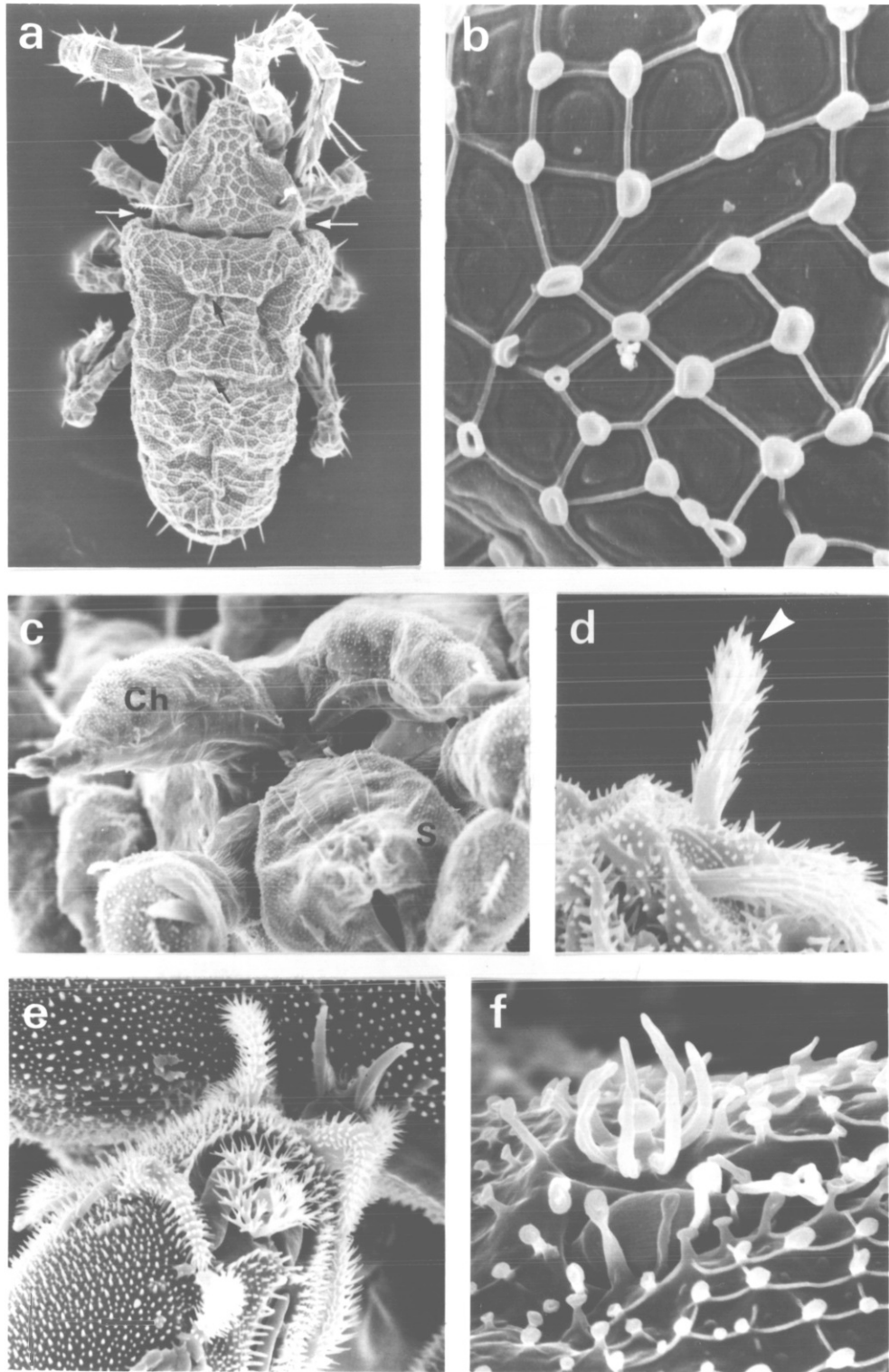


Fig. 18. Rhagidial organs and famuli:

- (a) *Eupodes alaskanensis*, tarsus II, famulus, arrowed, and rhagidial organ (x5000).
- (b) *Linopodes* sp., tibia I, distal rhagidial organ and famulus, arrowed (x9000).
- (c) *E. alaskanensis*, tibia I, famulus (x9833).
- (d) *Coccorhagidia macrostella*, tarsus II, elaborate famulus (x8150).
- (e) *Linopodes* sp., rhagidial organ and famulus in pit (x4900).
- (f) *Alloeupodes interruptus*, tibia II, rhagidial organs arrowed (x3917).
- (g) *Caleupodes reticulatus*, tibia I, rhagidial organ arrowed (x1150).

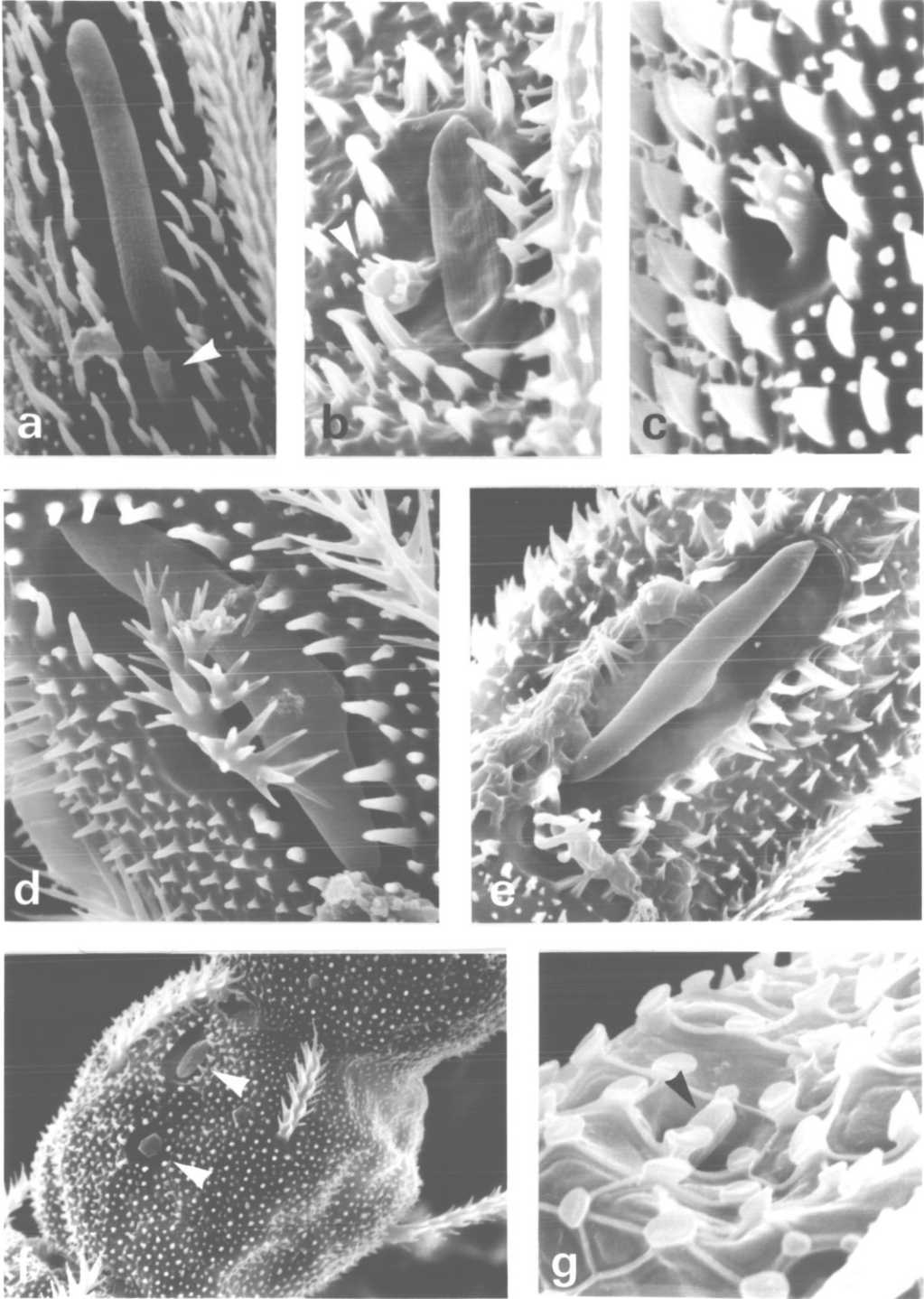


Fig. 19. Solenidia:

- (a) *Penthalodes ovalis*, tarsus I, semi-erect
rhagidial organs arrowed (x2400).
 - (b) *Cocceupodes* sp., tarsus I, rhagidial organ (x10389).
 - (c) *P. ovalis*, tarsus I, rhagidial organ arrowed (x4000).
 - (d) *Caleupodes reticulatus*, tibia II, rhagidial organ (x11481).
 - (e) *P. ovalis*, tibia II, rhagidial organ and erect
solenidion (x3488).
 - (f) *P. ovalis*, genu III, distal papilla (x4000).
 - (g) *Coccorhagidia macrostella*, genu I, erect solenidion (x13537).
- ro = rhagidial organ, sol = erect solenidion.

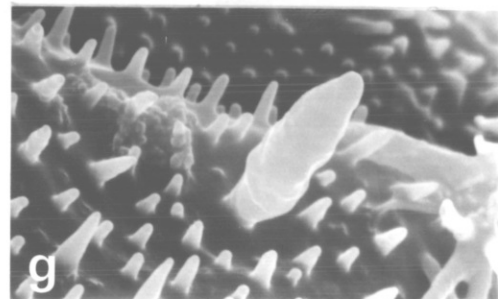
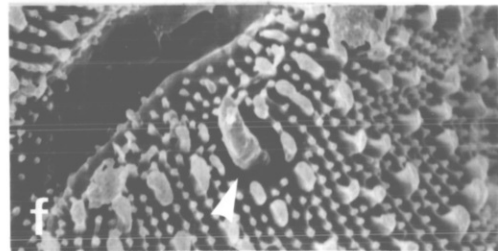
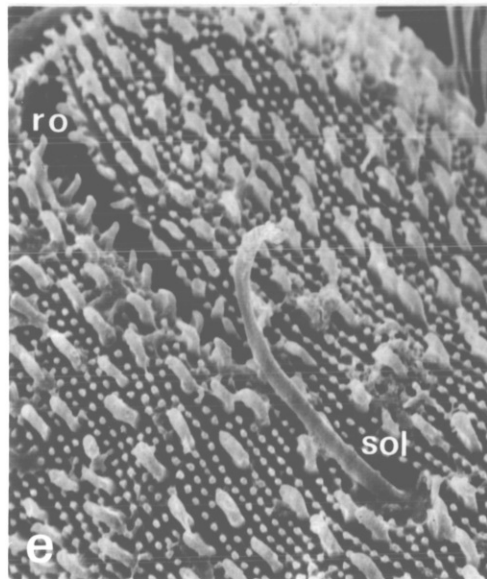
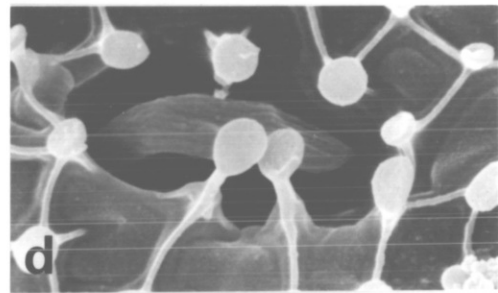
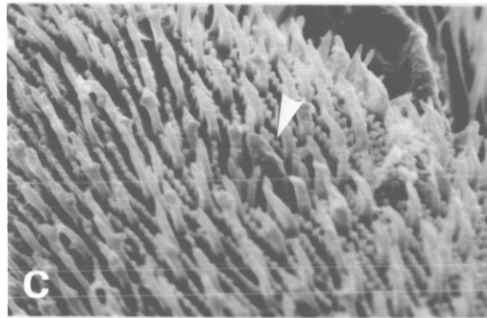
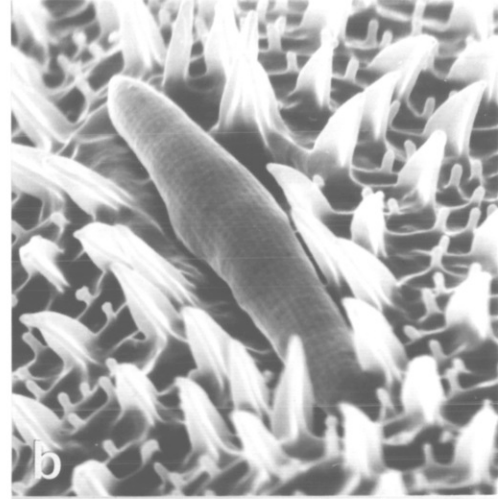
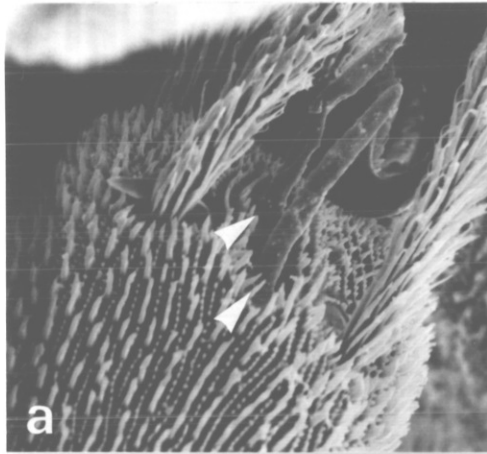


Fig. 20. Prodorsal trichobothria and bothridia:

- (a) *Coccorhagidia macrostella*, clavate median trichobothrium (x1600).
 - (b) *Cocceupodes* sp., bothridium of median trichobothrium (x10714).
 - (c) *Rhagidia* sp., bothridium of internal vertical seta (x9000).
 - (d) *C. breweri*, bothridium of internal vertical seta (x11688).
 - (e) *Eupodes alaskanensis*, naso and internal vertical setae (x1833).
 - (f) *C. breweri*, naso and internal vertical setae (x1525).
- B = bothridium, N = naso, T = trichobothrium.

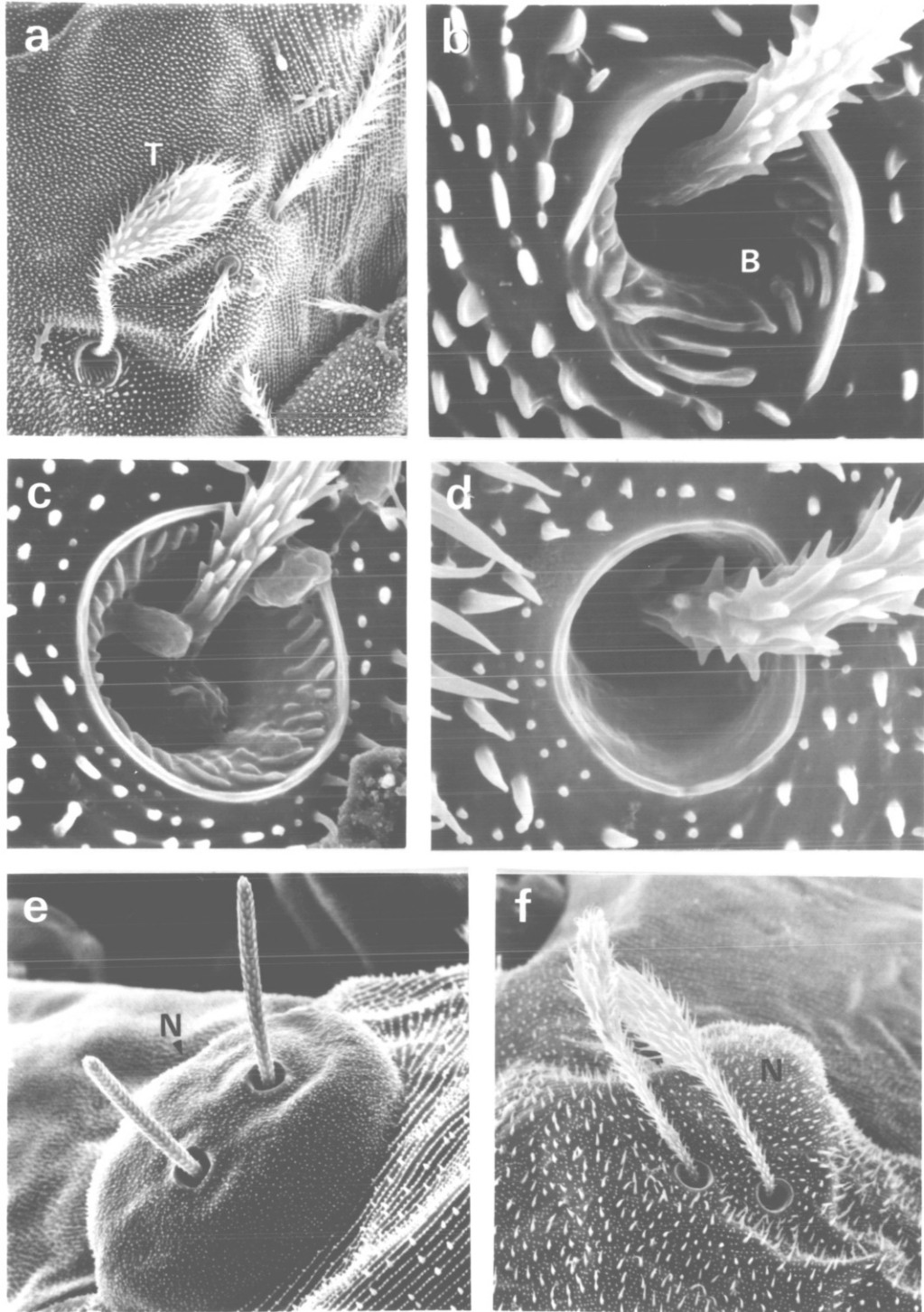


Fig. 21. Lyrifissures:

- (a) *Caleupodes reticulatus*, *im* (x7368).
- (b) *C. reticulatus*, *ih* (x6395).
- (c) *Cocceupodes trisetatus*, *ip* (x8000).
- (d) *Rhagidia* sp., *im* (x5950).
- (e) *Stereotydeus villosus*, *im* (x2700).
- (f) *Eupodes alaskanensis*, *ia* (x4133).

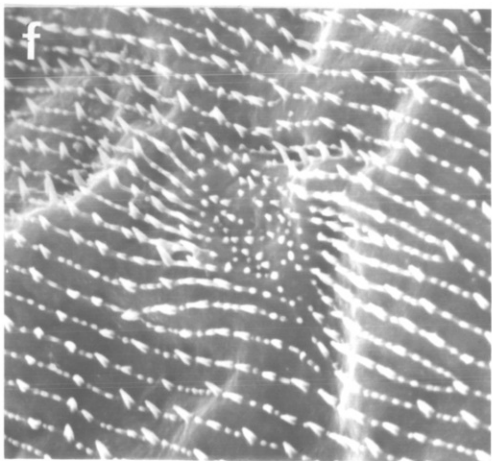
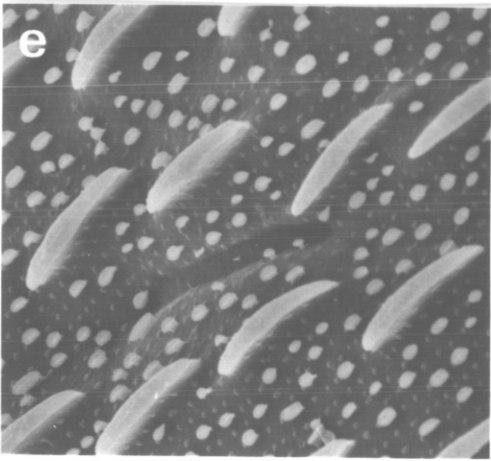
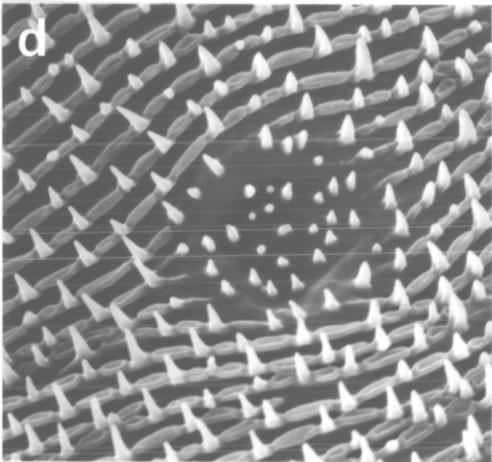
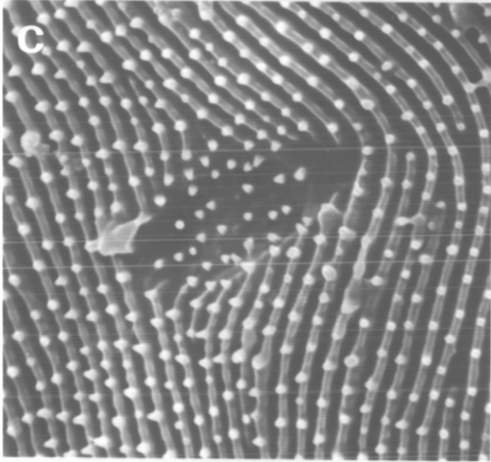
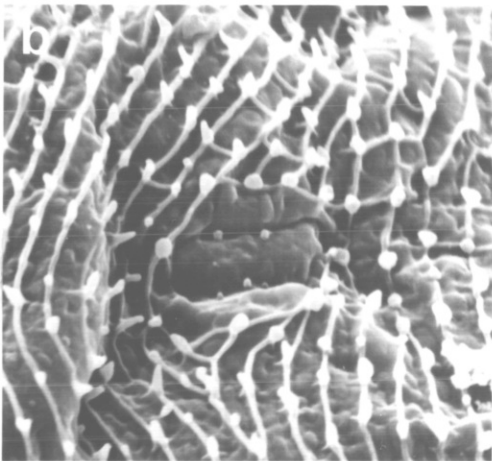
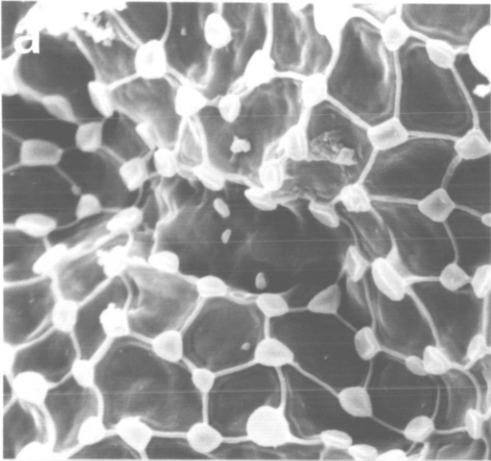


Fig. 22. Gnathosoma:

- (a) *Eupodes alaskanensis*, subcapitulum, ventral aspect (x809).
- (b) *Rhagidia* sp., subcapitulum, ventral aspect, adoral seta arrowed (x360).
- (c) *Penthaleus minor*, tip of subcapitulum, adoral setae arrowed (x2800).
- (d) *E. alaskanensis*, subcapitulum, lateral view (x5000).
- (e) *Caleupodes reticulatus*, tip of subcapitulum, adoral setae arrowed (x4942).
- (f) *Stereotydeus villosus*, chelicera, movable digit arrowed (x2375).

C = chelicera, S = subcapitulum.

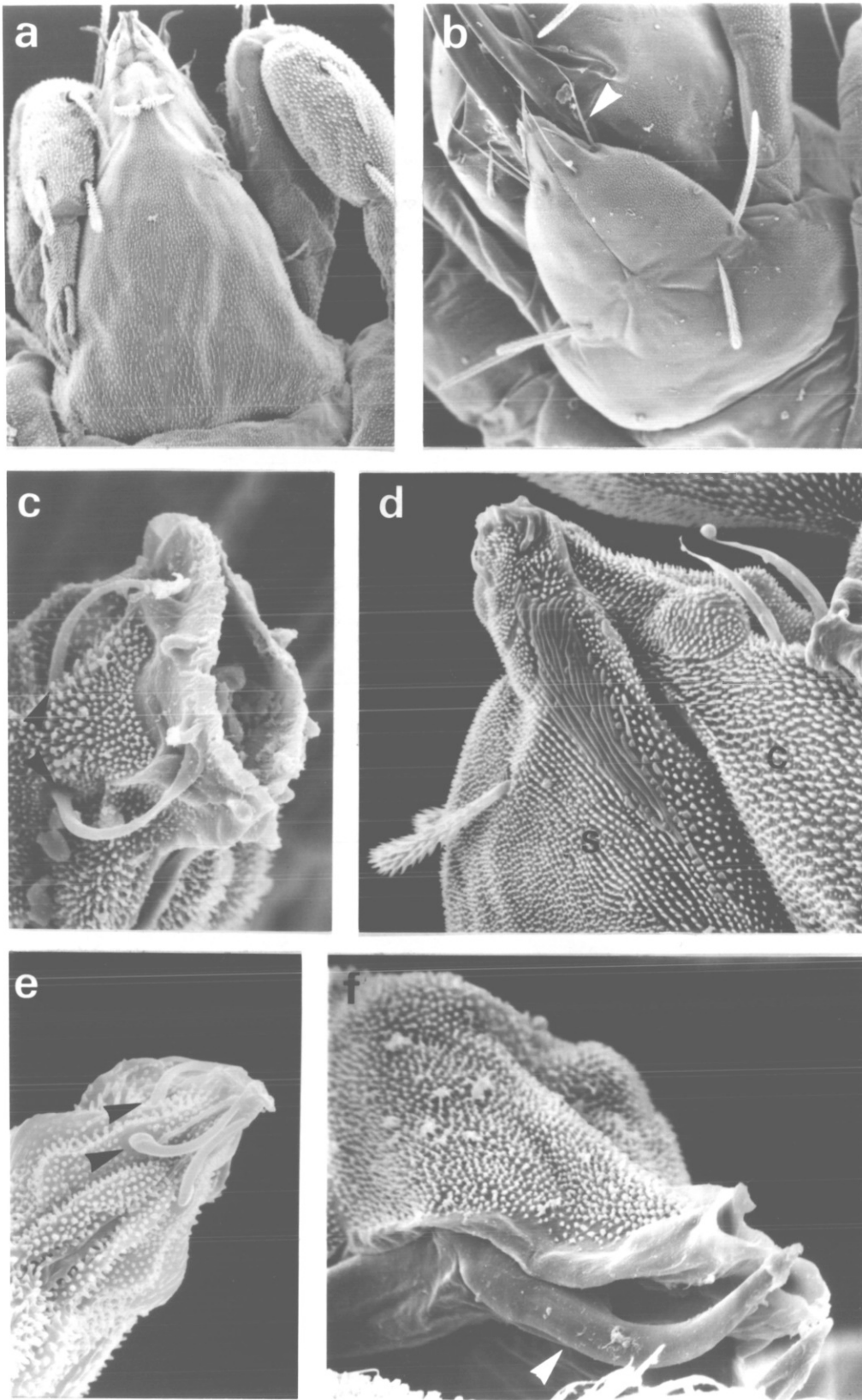


Fig. 23. Chelicerae, palps and supracoxal setae:

- (a) *Cocceupodes* sp., cheliceral seta, *cha* (x12200).
- (b) *Rhagidia* sp., chelicera and palp (x610).
- (c) *Penthalodes ovalis*, chela (x2115).
- (d) *Eupodes alaskanensis*, palp tibiotalar, spiralled 1' arrowed (x2529).
- (e) *Penthaleus minor*, strongly hooked movable digit (x872).
- (f) *Caleupodes reticulatus*, leg I, supracoxal seta (x11090).
- (g) *Alloeupodes interruptus*, leg I, supracoxal seta (x12660).

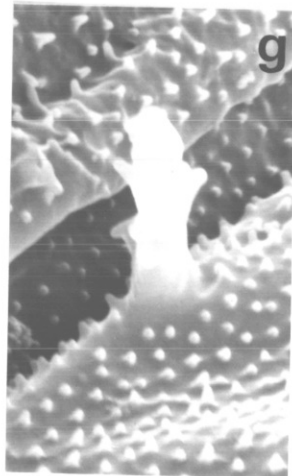
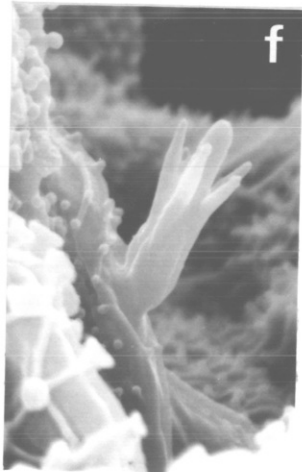
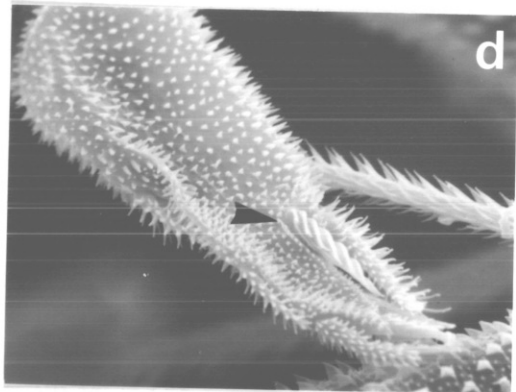
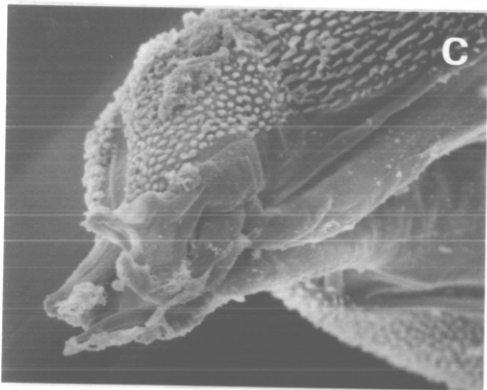
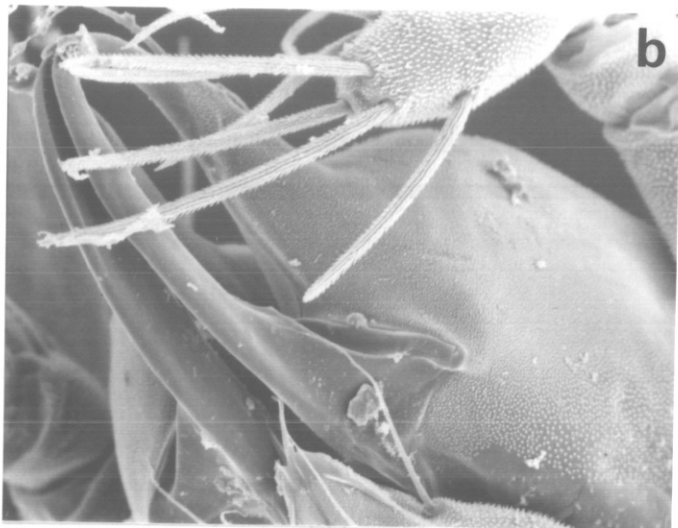
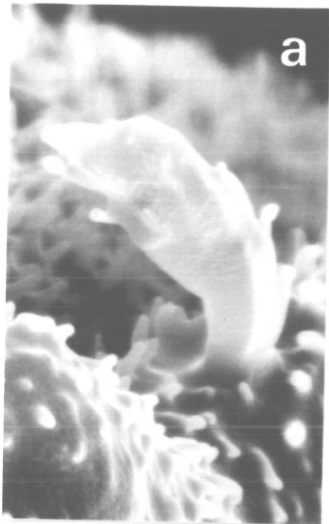


Fig. 24. Anus and genitalia:

- (a) *Penthaleus minor*, anus (x1145).
- (b) *Cocceupodes* sp., genital area, retracted genital papillae arrowed (x1321).
- (c) *Stereotydeus villosus*, genital shields (x440).
- (d) *Eupodes alaskanensis*, everted genital papillae (x2200).

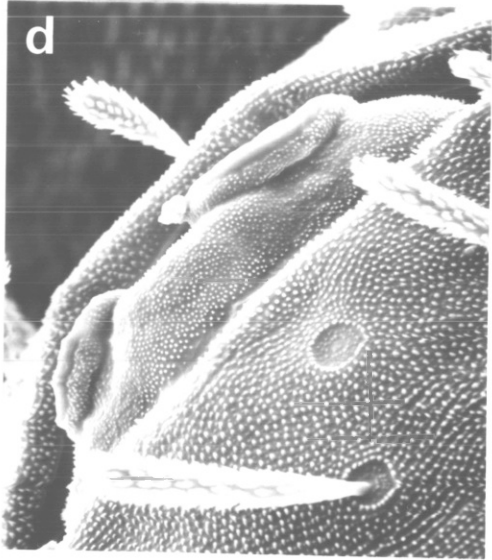
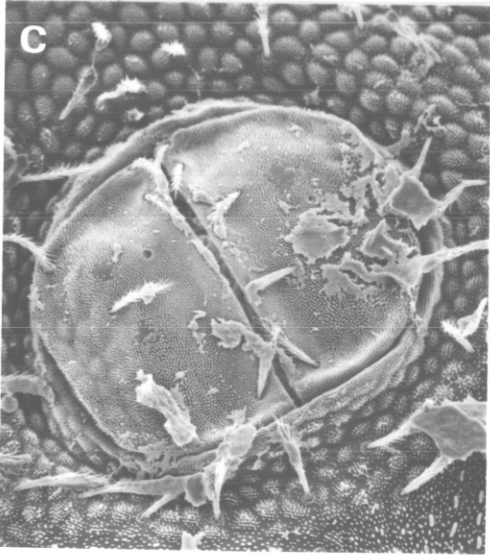
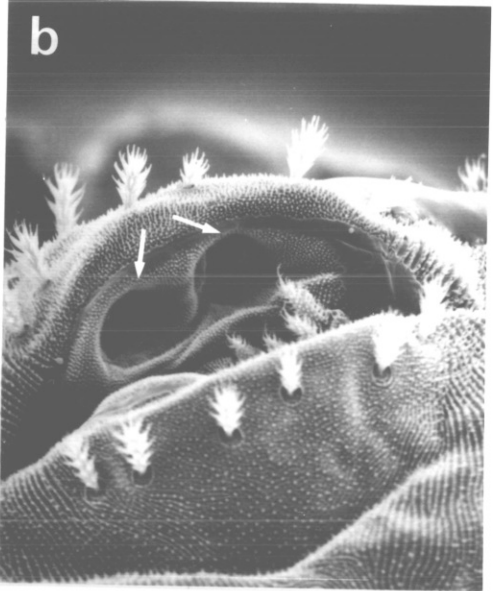


Fig. 25. Anal region:

- (a) *Caleupodes reticulatus*, adult (x2314).
- (b) *Coccorhagidia macrostella*, adult (x3140).
- (c) *Cocceupodes trisetatus*, larva (x4034).
- (d) *Penthalodes ovalis*, adult (x1870).

Ad/ad = adanal, PS/ps = pseudanal.

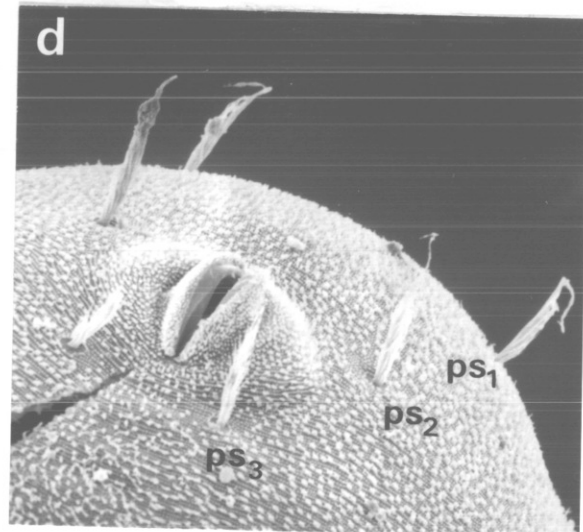
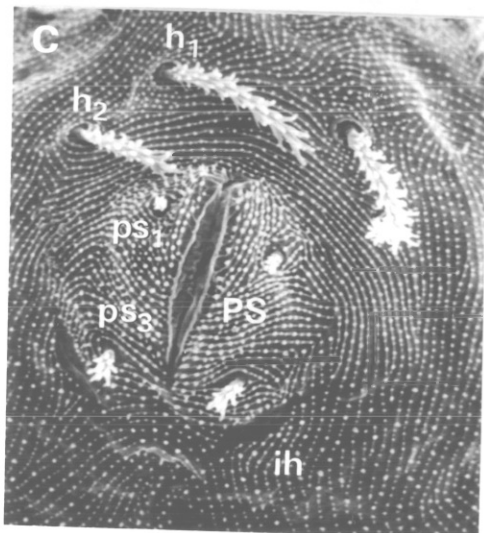
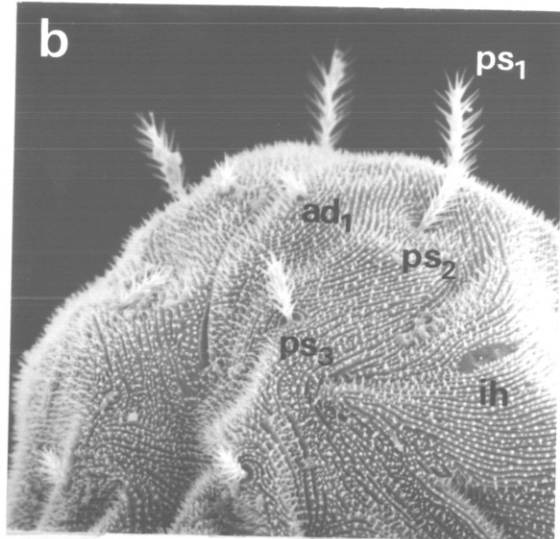
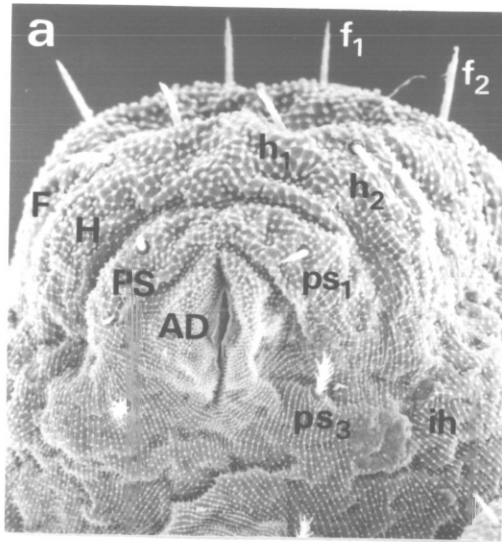


Fig. 26. Leg articulations and subdivision, *Eupodes alaskanensis*:

- (a) leg I, trochanteral-femoral articulation, dorsal aspect (x2166).
- (b) leg I, trochanteral-femoral articulation, lateral aspect (x1989).
- (c) leg II, dorsal tibial-tarsal articulation (x2890).
- (d) leg I, trochanteral-femoral articulation, ventral aspect (x2345).
- (e) leg IV, femoral-tibial articulation (x2065).
- (f) leg I, femur, crease in integument indicating subdivision of segment arrowed (x1895).

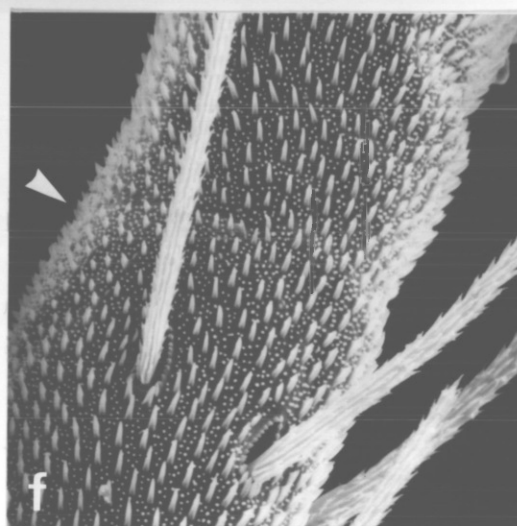
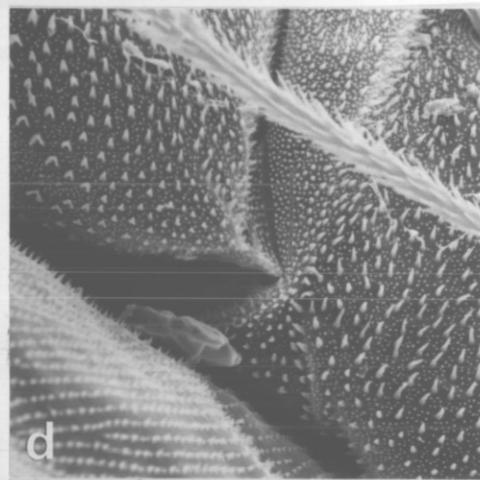
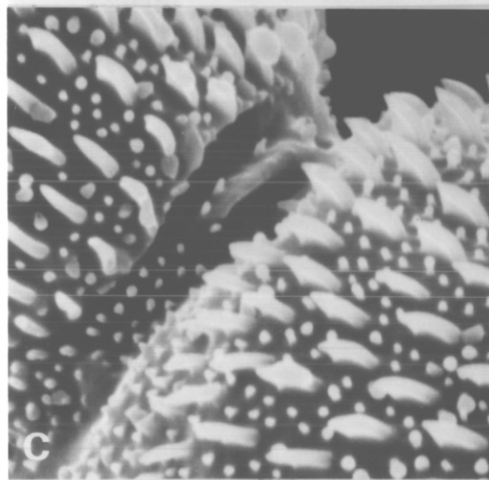
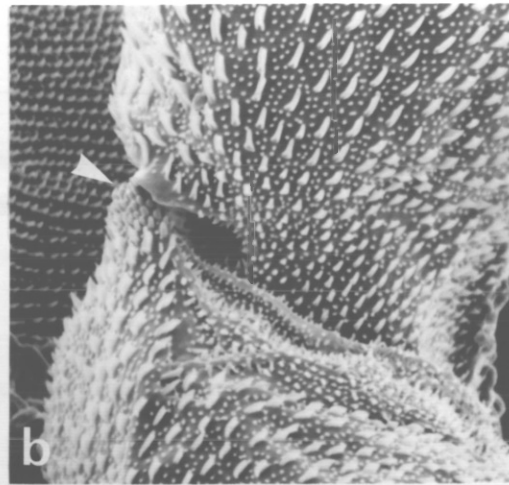
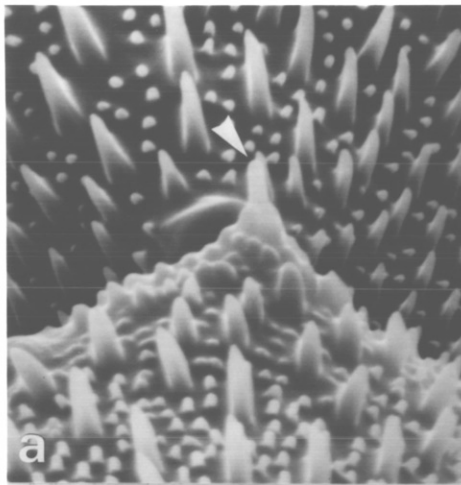


Fig. 27. Apotele:

- (a) *Fenthaleus minor*, leg I (x673).
 - (b) *Coccorhagidia macrostella*, leg I, empodial claw
arrowed (x892).
 - (c) *Rhagidia* sp., leg II (x540).
 - (d) *Cocceupodes* sp., leg I, reduced apotele (x890).
- Cl = claw, Em = empodium.

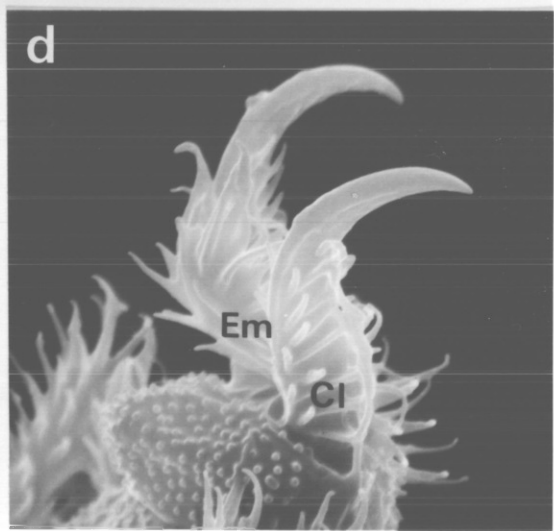
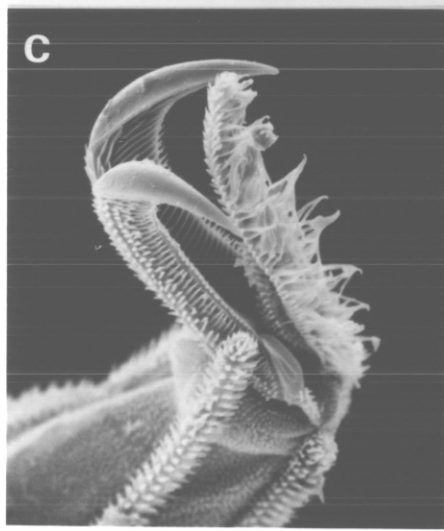
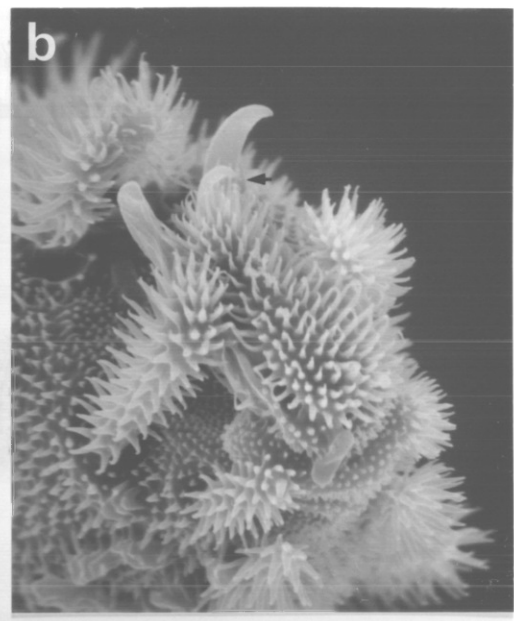
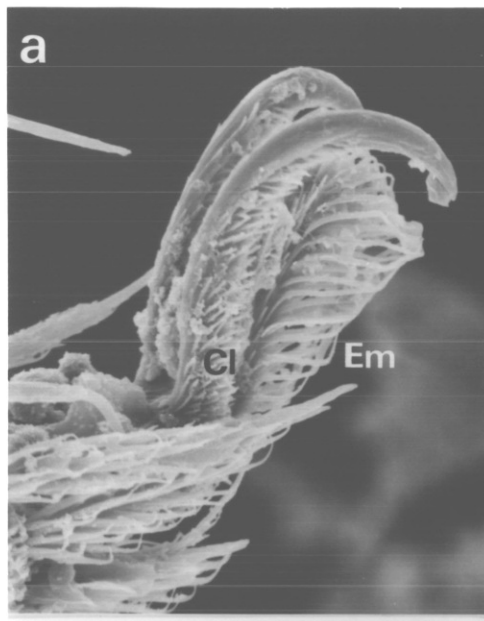


Fig. 28. Claparède organs and genital papilla:

- (a) *Penthaleus* sp., ventral aspect, Claparède organ arrowed (x540).
- (b) *Penthaleus* sp., Claparède organ, smooth dome of organ covered by cap arrowed (x5400).
- (c) *Cocceupodes* sp., ventral aspect showing location of Claparède organs (x1120).
- (d) *Cocceupodes* sp., Claparède organ, smooth under-surface of cap arrowed (x6280).
- (e) *Eupodes* sp., Claparède organ, smooth dome of organ partially covered by cap arrowed (x4500).
- (f) *E. alaskanensis*, everted genital papilla (x4535).

C = cap.

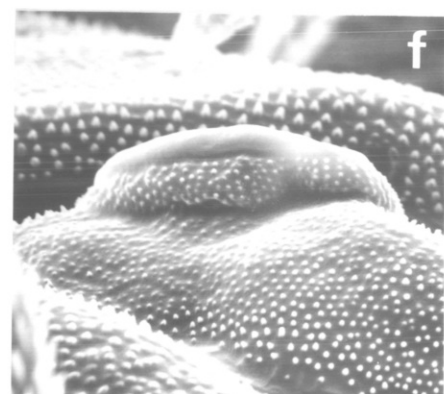
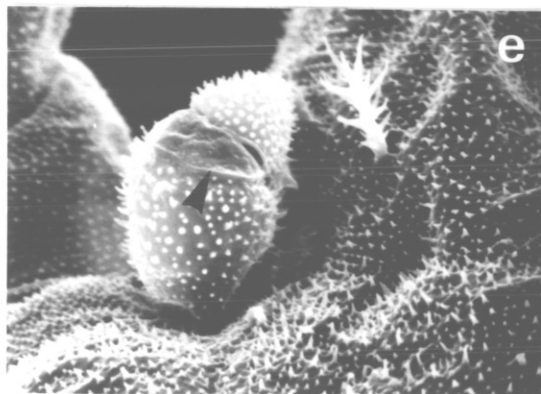
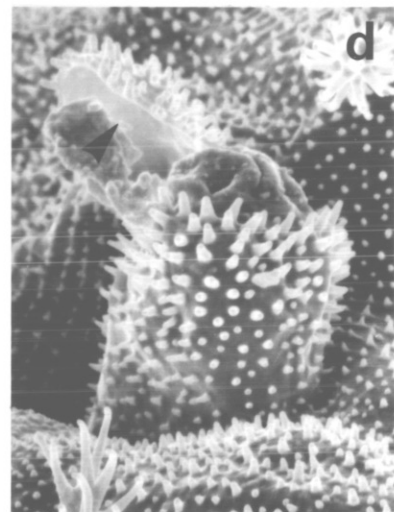
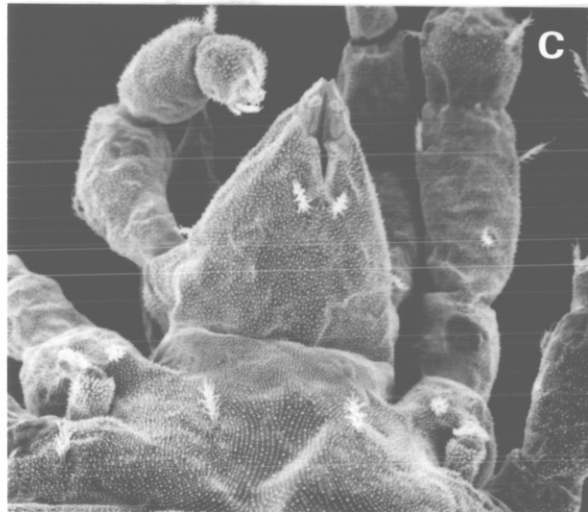
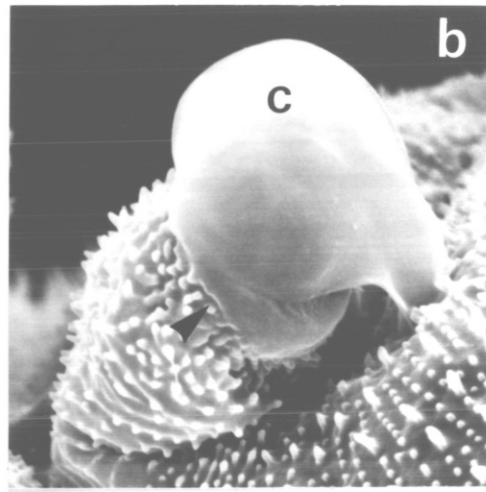
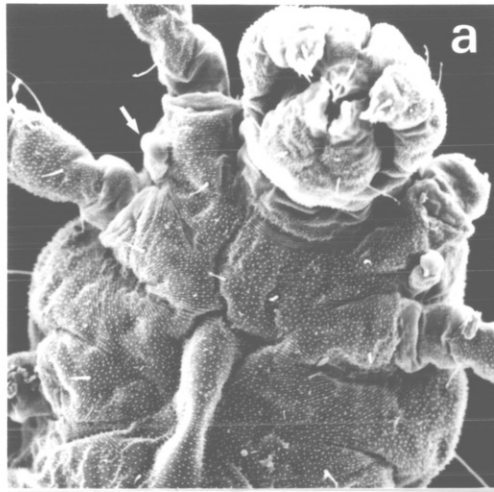

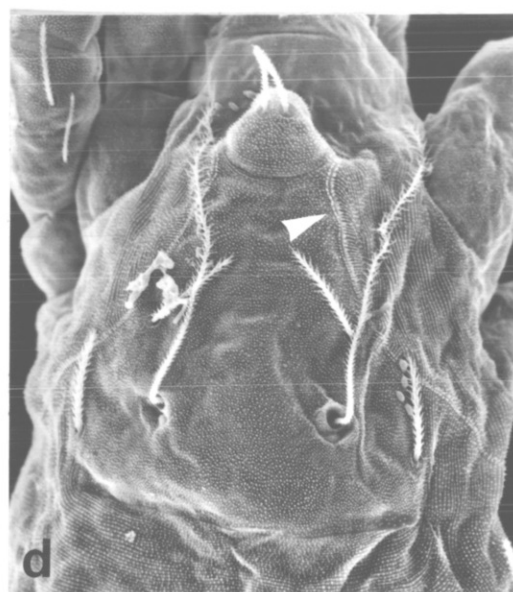
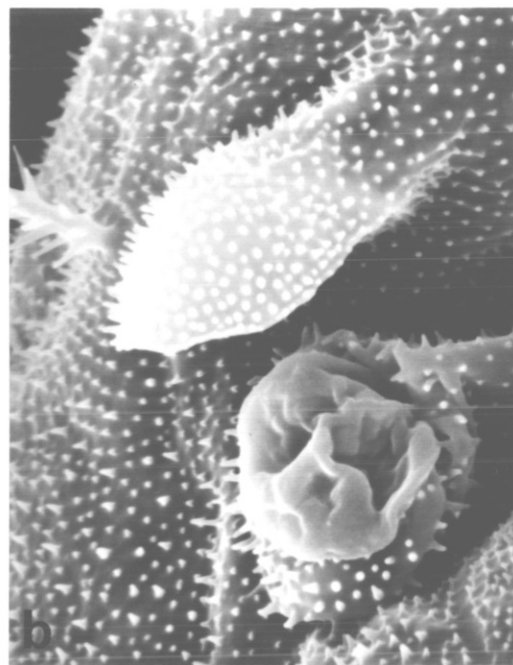
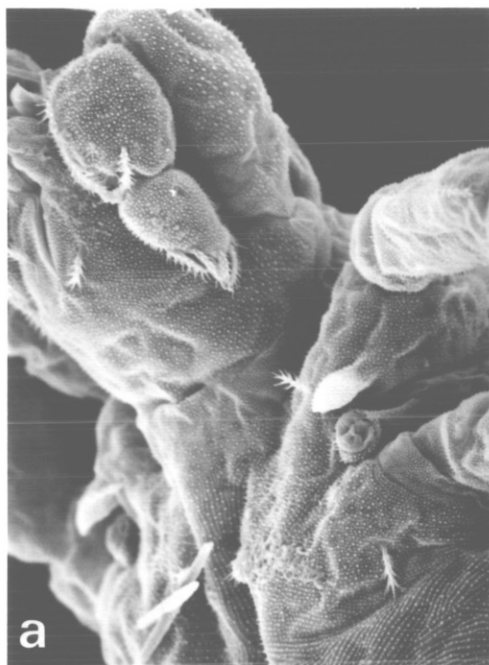


Fig. 29. Immature stages:

- (a) *Cocceupodes* sp., ventro-lateral aspect showing location of Claparède organ and cap (x1343). 
- (b) *Cocceupodes* sp., Claparède organ withdrawn (7105).
- (c) *Cocceupodes* sp., lateral aspect of withdrawn Claparède organ (x8000).
- (d) *Rhagidia* sp., tritonymph, prodorsum, dehiscence line arrowed (x996).



8. SYSTEMATIC ANALYSIS AND CLASSIFICATION

8.1 INTRODUCTION

There are four principal methods of systematic analysis: 1) traditional; 2) evolutionary; 3) phenetic or numerical (as numerical techniques are now used in other areas of taxonomy, the term phenetics is preferred); 4) cladistic or phylogenetic (the former term is used as 'phylogenetics' can be confused with the evolutionary methods).

The first two methods overlap to a large degree and the terms tend to be used synonymously. Neither has a strict theoretical basis, but instead relies on the intuition and experience of the individual worker to group taxa. Traditionalists, however, are accused of just being concerned with producing a cataloguing system for organisms. Evolutionary systematists, by contrast, recognize organisms as being products of evolution and aim to produce classifications which also infer evolutionary processes.

The phenetic approach considers organisms as they are seen in the present and places importance on the amount of sharing of any character state, *i.e.* the form in which a character occurs. Within a selection of taxa, therefore, those with the most character states in common will be considered most closely related.

Lastly, the cladistic method, like evolutionary systematics, sees organisms as products of evolution but it is only concerned with the possession of shared character states which are derived from the primitive ancestral state. Thus, in a selection of taxa, those sharing the largest number of derived characters (apomorphies) will be considered

most closely related. Primitive characters (plesiomorphies) are not used to define groups in cladistic analyses.

There is much argument about the objectivity and the quality of the information provided by the various methods (see section 8.4 for a more detailed account), such that they have tended to develop schools of protagonists rather than being used in complimentary ways.

A survey of the eupodoid literature highlights three problems that arise within the superfamily, namely, the ill-defined generic boundaries, the inconsistent use of definitive characters and the absence of any comprehensive study of interrelationships. The only author who has addressed the latter question in any detail is Zacharda (1980) who postulated the phylogenetic relationships between the genera of the family Rhagidiidae.

The main purpose of the present study is to identify the eupodoid taxa collected in Britain, two intrinsic parts of which are the establishment of supra-specific boundaries and the identification of diagnostic characters. Systematic analyses of mites have predominantly been achieved by traditional means, but phenetic methods were introduced some years ago (Sheals 1963, 1969) and are still in current use (Paschoal & Johnston 1982). More recently, however, cladistic analyses have been increasingly applied (Antony & Johnston 1984, OConnor 1984, 1984a, Niedbala 1986). The results produced by these methods apparently satisfied the respective workers who carried out the studies. Consequently, it was decided to apply both phenetic and cladistic methods to the Eupodoidea in an attempt to assess which gave the most satisfactory classification and to compare the results with those obtainable through a traditional approach. To permit a proper study of variability throughout the superfamily, the British fauna has been complemented by inclusion of the type species of

genera and, in some cases, other representatives of those genera not found in Britain.

Clarification of concepts used

With the emergence of the various schools of systematics, the definitions of a number of traditionally established concepts have become ambiguous. New terms have been devised for some of these alternative definitions (see Holmes (1980) for a detailed account) while the usage of others is still ambivalent. For example, the concept of homology, that like be compared with like, is central to taxonomic analyses. Despite this fundamental importance, the term has not been satisfactorily defined for all schools of thought (Holmes 1980, Patterson 1982). Essentially, two concepts of homology can be identified; that which regards common ancestry as the basis is used by cladists, while that which stresses similarity in structure and position is favoured by pheneticists. When determining homologies in the Eupodoidea for systematic analyses, the respective concepts were applied to their particular schools.

The usage of other concepts used in this study is specified when the term first appears.

8.2 PHENETIC ANALYSIS

The two methods frequently applied in phenetic studies are principal components analysis and principal co-ordinates analysis. The former constructs a multi-dimensional plot of the taxa in question (the operational taxonomic units, abbreviated to OTU) using pairs of characters as axes and requires that all the data be quantitative and that no missing values occur. Since, in this study, both quantitative and qualitative characters were to be used and it was known that there would be some missing values, the use of a principal co-ordinates analysis was chosen in preference.

Instead of a multi-dimensional plot using the characters as axes, principal co-ordinates analysis calculates the percentage of overall similarity between each pair of OTUs, *i.e.* the average of the similarity for each character. The OTUs are then plotted on a multi-dimensional graph, the distance between them on the plot being approximately inversely proportional to their similarity. One disadvantage of principal co-ordinates analyses is that, since the plot is constructed from the table of similarities between the OTUs and does not use the variates as axes, it is less easy to determine which characters are responsible for groupings. In the present study, this was later discerned by instructing the computer to plot the co-ordinates of each character separately, thus graphically displaying the distribution of the different character states.

Serious distortion of the principal co-ordinates plot occurs if there are many missing values in the data matrix. This is a result of a calculation being ignored if one of the values is missing. The measurement of overall similarity is, thus, calculated on a reduced data set.

8.2.1 Principal co-ordinates analysis of the Eupodoidea

The analysis was carried out on a PDP 11/24 microcomputer using the program TAXON. Apart from the multi-dimensional ordination of OTUs referred to above, this program also applies a cluster analysis to the data. This attempts to determine homogeneous groups of OTUs and, consequently, produces a hierarchy of these clusters. TAXON uses an agglomerative method for doing this, i.e. the OTUs are gradually linked to form groups by a series of fusions rather than, as in the alternative divisive method, the OTUs are separated into smaller and smaller groups by successive divisions.

The two methods detailed above respectively result in what Beckner (1959) called polytypic and monotypic groups, although, as these terms were already established in systematics, Sneath (1962) suggested substituting 'polythetic' and 'monothetic'. The polythetic groups produced by agglomerative methods are based on a complete set of recorded characters and the members of each group so formed will share a number of character states, no one of which is either essential or sufficient to define group membership. The disadvantage attributed to this type of assemblage is that it is difficult to define. The inherent advantage, however, is the flexibility of definition which prevents specimens aberrant in one character from being wrongly classified. Monothetic groups, by contrast, are produced by successive divisions using a sequence of characters. Each group is, therefore, rigidly defined by a single character state or combination of states that are present in all the members of that group but absent in the members of others.

In total, TAXON produces the following: a summary of statistics for each character; a similarity matrix; a minimum spanning tree; a single-

linkage cluster analysis; a list of the nearest neighbours of each OTU and, finally, the principal co-ordinates are calculated and plotted.

Summary statistics.

Using the statistics program MINITAB, the computer calculates the mean, maximum and minimum values, standard deviation and standard error of the mean and the number of missing values for each character. These data are useful to the operator mainly for checking that the data has been entered into the computer correctly and that the right format has been used.

Similarity matrix.

The computer calculates the percentage similarity between each OTU and every other OTU according to Gower's similarity index (Gower 1971).

The computer must be instructed on how to treat the comparisons of each character, the choice depending on how the information of the character has been presented. There are five alternative instructions (x_{ik} means the value of the k^{th} character for the i^{th} OTU, similarly x_{jk} means the value of the k^{th} character for the j^{th} OTU):

1. Qualitative character

As type 2, but ignore this character when it has state 0 on both OTUs, i.e. when $x_{ik} = x_{jk} = 0$

2. Qualitative character

$x_{ik} = x_{jk}$ similarity = 100%

$x_{ik} \neq x_{jk}$ similarity = 0%

3. Quantitative character

$$\text{Similarity} = \frac{(1 - |x_{ik} - x_{jk}|)}{\text{range}(k)} \times 100\%$$

i.e. One, minus the difference between the two values divided by the range of values that the kth character takes in the data set, expressed as a percentage.

4. Quantitative character

As type 3, but ignore the kth character when both OTUs have state 0, i.e. when $x_{ik} = x_{jk} = 0$

5. Type 0

Ignore this character.

As can be seen from the above formulae, quantitative characters are not so 'all or nothing' as qualitative ones. In the continuous sequence of states of a quantitative character, OTUs with states close together on the scale will be accorded greater similarity than OTUs scored at opposite ends of the scale.

To prevent ambiguous information from being entered, it is important to give both the right instruction to the computer and to consider the formulae when devising the character states and their codings. For example, if the following was used:

Internal vertical setae: form 0 filiform

1 not filiform - it would have to be

entered as a type 2 instruction, since, if it was read as a type 1, two OTUs with filiform internal vertical setae would be treated as dissimilar because the calculation would be ignored in the analysis. If the character states were reversed, i.e. 0 not filiform, 1 filiform, then it must be read as a type 1 since, otherwise, OTUs with subclavate or

capitate setae will be treated as the same. In this study, however, this character was coded to give more information by regarding it as a quantitative character with the following sequence of states:

Internal vertical setae: form 0 filiform
 1 subclavate
 2 clavate
 3 capitate

The computer was instructed to read this as a type 3 since it would be meaningful to include pairs of OTUs with state 0 in the calculation of similarity.

If, as in this study, the similarity matrices are large, it is difficult to immediately identify groupings of OTUs. To make the data more easy to assimilate, OTUs can be arranged in the order in which they appear in the single linkage cluster analysis and the various ranges of percentage similarities represented by different symbols (Figs 35, p.166, & 40, p.179).

Minimum spanning tree.

This is presented as a branching diagram (see Fig. 31) which summarizes the information in the similarity matrix. The first step joins the two most similar OTUs (in this study OTU2 and OTU4). Then, step by step, an OTU not in the tree is joined to the OTU already included to which it is most similar. This continues until all the OTUs are in the tree.

Single-linkage cluster analysis.

This is derived from the minimum spanning tree and produces a dendrogram showing the merging of clusters at successive levels (Fig. 31, p.153).

The step length between successive levels of the dendrogram is chosen by

the worker. In this study, the step size chosen was 1%. Each OTU is regarded as a 'cluster' of one. At any level of percentage similarity, if any OTU in one cluster has a similarity greater than that level to any OTU in another cluster, the two clusters are merged at that level. Then the next level down is checked until finally all the OTUs are in one cluster.

As mentioned above, two clusters may join together simply because a single member of one of the clusters has a high similarity to a single one in the other cluster and there is no guarantee that all the members of the clusters are similar to one another. However, a check of anomalous groupings can be made using the next function of the program, the nearest neighbours list.

The dendrogram printed out for the single-linkage cluster analysis is usually rationalized by drawing phenons on it. These are lines drawn at arbitrary levels of similarity in order to divide the dendrogram into sensible groupings of OTUs which signify clusters of different ranks.

Nearest neighbours list.

This is another summary of the similarity matrix. In this study, the six nearest neighbours, *i.e.* the six most similar OTUs, were listed for each OTU.

This list is useful to check the coherence of clusters. As an example, OTUs 1, 2, 3 are joined to OTUs 3, 4, 5 in the single-linkage cluster. If this is a significant grouping then OTUs 3, 4, 5 should be listed as nearest neighbours of 1, 2, 3 and *vice versa*.

Principal co-ordinates analysis.

Finally, the computer calculates the principal co-ordinates for each OTU in multi-dimensional space. The distances between the OTUs are roughly inversely proportional to the similarities between the OTUs, with the most similar OTUs, therefore, close together and dissimilar ones more widely separated. The multi-dimensional nature of the plot obviously prevents all aspects of it from being portrayed in two-dimensions, such as on a single sheet of paper. The computer, therefore, presents the best two-dimensional view by choosing the two vectors for axes which account for the most variance, placing the second axis at right angles to the first, and then plotting the points representing the OTUs against them.

Usually, only the first three or four axes are important, subsequent values accounting for little of the total variation. It is, however, possible for OTUs dissimilar in a direction not represented by the principal co-ordinates axes to be projected on to close positions on the plot, but, again, groupings can be checked by referring to the nearest neighbours list. As a further check, the OTUs can be joined on the plot using differentiated lines to represent the linkages of the minimum spanning tree (Fig. 35, p.167). Plots of principal co-ordinates are useful for providing a visual indication of clusters of OTUs.

8.2.2 The data matrix

Operational Taxonomic Units (OTUs)

Each OTU represents one species. In the current study a practical species concept was used wherein a number of specimens which possessed a unique character state or combination of states was regarded as a

species. This concept is intended to conform to the definition of Wiley (1981):

'An evolutionary species is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.'

The OTUs used comprise 39 of the 40 eupodoid species described in Section 10 (one species was found after phenetic analyses had been completed) plus, where appropriate, the type species of genera. In addition, where characters of the type species of genera not found in Britain could not be clearly discerned, certain other representatives of the genus were included. This category largely comprised the members of supra-specific taxa described by Zacharda in his monograph of the Rhagidiidae (Zacharda 1980). Although he has subsequently described further taxa (Zacharda 1982, 1983), the inclusion of those from the monograph were regarded to be sufficient to test his classification. The list of OTUs and the origin of their data is given in Table 6 which, to assist with the interpretation of the results, is given in the fold-out on page 181. New taxa found in the British fauna were assigned to traditional concepts of genera and suffixed with a specific reference number. Eventual names of these taxa can be obtained from Table 10 (p. 242).

The characters

There are many aspects of an organism from which characters can be chosen, for example, internal anatomy, external morphology, physiology, biochemistry, genetics, ecology and behaviour. In reality, however, the number that can be used are limited by practical considerations such as the state of the material that can be studied and the equipment available

for use. In the present study, as in most other taxonomic works, the material was in a preserved state and therefore afforded the opportunity to observe external morphological features.

Even when limiting oneself to the external morphology, there is an enormous number of characters that could be recorded and used to construct a classification, even in mites as apparently similar to one another as the members of the Eupodoidea. Although it is desirable to include as many characters as possible, it would be impractical to include every one in a single analysis. Indeed, some would make no contribution since they can be identified as common to all OTUs, whilst a number only occur in association with one other and, as such, are termed redundant characters. Others which occur uniquely within the group are excluded as they make no contribution to overall similarity. Inclusion of these types of characters could, apart from taking up unproductive space on the computer, bias the calculation of overall similarity.

In this study, in the search for diagnostic characters, an attempt is made to introduce features from all aspects of the external morphology, the final list of 90 characters can be seen in Table 5. The initial list contained many more of the theoretically possible characters but some were subsequently excluded. Numbers of leg setae were omitted because they could not be discerned in the majority of OTUs where only type material was examined. To include so many missing values in the analysis was considered to risk distorting the results. Other characters were excluded because they could not be confidently scored. For example, the supracoxal setae were known to vary somewhat in ornamentation but those considered smooth under the light microscope had been shown to be weakly papillate under the scanning electron microscope. Since these

setae had not been observed in all species in this way, it was felt better to omit this character.

Coding of character states and computer treatment of data.

When coding the forms in which the various characters occurred, care was taken to avoid introducing ambiguities and to include the greatest amount of information in their expression.

As mentioned previously, both quantitative and qualitative characters were used in this study. Quantitative characters such as body length and setal numbers are given in absolute numbers, but those such as length of setae, legs and so on, are given as a ratio (see Table 5 for details). The ratios ensure that these types of characters would be compared on the same scale. Otherwise, two OTUs in which the lengths of leg I are the same would be scored as being similar but, in one, the length could be one and a half times the body length while, in the other, only three-quarters of the length. Body lengths were given to the nearest micron, ratios were given to two decimal places.

Weighting of characters

To weight a character is to give it greater or lesser importance than another used to produce a classification. There are several ways of weighting characters. Indeed, the initial choice of characters to be used is itself a method of weighting. Inevitably, some characters are included while others are excluded from the analysis; therefore, a subset of the potential characters is produced. This type of weighting is selection weighting. At the same time, it might be decided to reject other potential characters for the reasons given above, *i.e.* that they are

invariant of if they are correlated with previously selected characters. This is rejection weighting. Both of these were applied in the present study.

There are two other types of weighting - *a priori* and *a posteriori*. The former means that, amongst the characters chosen, some are considered more important than others, for example emphasis is placed on characters known to be good diagnostic characters in other taxa. This approach has been criticized because it tends to bias the resulting classification towards that which the worker would like to produce before the data is even analysed and so reduces objectivity.

A posteriori weighting, by contrast, is applied in retrospect, after the analysis has been completed and a classification constructed. For example, if, after the data have been analysed, one wishes to identify a specimen not included in the original analysis, it is examined for the characters which proved more useful than others in defining taxa. Since this choice is made after the analysis, it does not influence it or the clustering of the taxa concerned.

Since the aim of this study was both to construct a classification for the Eupodoidea and to investigate the characters which have most influence on its formation, the characters were given equal weight.

Table 5. Characters and character states used in phenetic analyses.

* character omitted in Run 1 of the analyses.

<u>Character</u>	<u>State</u>
* 1, Body length;	in microns
* 2, Body width;	as proportion of body length
3, Prodorsal setae;	number
4, Opisthosomal setae;	number
5, Internal vertical setae; position;	0 on naso 1 at base of naso 2 posterior to naso
6, Internal vertical setae; length;	as proportion of body length
7, Internal vertical setae; form	0 simple 1 subclavate 2 clavate 3 capitate
8, Prodorsal trichobothria; form	0 simple 1 subclavate 2 clavate 3 capitate
9, External vertical setae; position	as proportion of distance from trichobothria to anterior of prodorsum
10, Scapular setae; position	as proportion of distance from trichobothria to anterior of prodorsum
11, c_1 ; length	as proportion of body length
*12, Coxa I; length of $/c$	as proportion of $/a$
13, Coxa III;	number of setae
14, Coxa IV;	number of setae
15, Genital setae;	number of setae
*16, g_1 ; length	as proportion of body length
17, Aggenital setae;	number of setae
18, Setae associated with anus;	number of pairs

*19.	Subcapitulum; length	as proportion of body length
*20.	Subcapitulum; width	as proportion of length
21.	Subcapitular seta (<i>sbc₂</i>); position	as proportion of distance from anterior of subcapitulum to level of (<i>sbc₁</i>)
*22.	Subcapitular seta (<i>sbc₁</i>); length	as proportion of (<i>sbc₂</i>)
23.	Chelicera;	number of setae
*24.	Chelicera; length of (<i>cha</i>)	as proportion of cheliceral length
25.	Chelicera; length	as proportion of body length
26.	Chelicera; length of movable digit	as proportion of cheliceral length
27.	Palp tibiotalrus;	number of setae
28.	Palp tibiotalrus; dimensions	0 length > 2,5 times width 1 length < 2,5 times width 2 width > length
*29.	Palp genu;	number of setae
30.	Palp genu; length	0 < tibiotalrus 1 = tibiotalrus 2 > tibiotalrus
*31.	Palp femur;	number of setae
32.	Leg I; length	as proportion of body length
33.	Tarsus I;	number of rhagidial organs
34.	Tibia I;	number of rhagidial organs
35.	Tarsus II;	number of rhagidial organs
36.	Tibia II;	number of rhagidial organs
37.	Trochanter IV;	number of setae
*38.	Leg femora; extent of subdivision	0 all completely 1 I & II partially, III & IV completely 2 all partially 3 absent
*39.	Naso; form	0 small rounded peak, not delimited 1 small delimited lobe 2 distinct delimited, roughly rectangular lobe 3 distinct peak 4 smooth semi-globe 5 free lobe

40.	Epirostrum;	0 absent 1 present
*41.	Sejugal furrow; form	0 absent 1 indistinct, represented by slight change in integument 2 distinct furrow
42.	Dorsal differentiation of idiososomal integument	0 absent 1 Y- or V-shaped indentations 2 with parallel longitudinal furrows on opisthosoma 3 with opisthosomal segmentation
43.	Raised prodorsal eyes;	0 absent 1 present
44.	Setae (c_2); position	0 level with (c_1) 1 level with (f)
45.	Setae (f_2); position	0 level with (f_1) 1 markedly posterior to (f_1)
46.	Setae (f_1); form	0 normal 1 trichobothridial 2 with bothridial base
47.	Lyrifissures; form	0 round 1 eye-like 2 slit-like
*48.	Coxae; arrangement	0 II and III separated 1 II and III contiguous
*49.	Coxae; delimitation	0 faintly but distinctly defined 1 distal margins only defined 2 strongly defined
*50.	Genital shields; delimitation	0 outer margins faint 1 outer margins with clear suture
51.	Genital setae; arrangement	0 in single file 1 g_4 lateral 2 g_5 lateral 3 other than above
52.	Anus; position	0 dorsal 1 terminal 2 subterminal
*53.	Anus; form	0 slit-like 1 circular
*54.	Seta (ps_1); position	0 dorsal 1 subterminal

55.	Adoral setae; number and length	0 four, minute 1 four, long 2 two, long
56.	Chelicera; form of fixed digit	0 reduced, terminating in shallow fork 1 reduced, terminating in 3-pronged fork 2 strongly hooked
*57.	Cheliceral setae; position <i>cha</i>	0 proximal to fixed digit 1 on fixed digit
*58.	<i>Chb</i> ; insertion point	0 in a depression 1 surface
*59.	Supracoxal setae;	0 absent 1 present
60.	Palp; terminal margin of tibiotalrusus	0 broadly rounded 1 not broadly rounded
61.	Palp; form of tibiotalrsal setae	0 homogeneous 1 heterogeneous
62.	Palp; form of tibiotalrsal solenidion	0 absent 1 rhagidiform 2 spiniform
*63.	Palp; form of genu	0 width and length <i>ca.</i> equal 1 length > than width
64.	Femur IV; form	0 slender 1 greatly enlarged
65.	Apotele I; form	0 greatly reduced 1 same form as others 2 greatly enlarged
*66.	Tarsus I; form of rhagidial organs	0 all L-shaped 1 all T-shaped 2 bridge-like
67.	Tarsus I; arrangement of rhagidial organs	0 in tandem, in confluent pits 1 in tandem, in separate pits 2 staggered longitudinally parallel 3 level longitudinally parallel 4 obliquely parallel 5 longitudinal 6 in tandem and parallel 7 not as above
68.	Tarsus I; famulus	0 absent 1 present
69.	Tarsus I; form of famulus	0 elaborately branched 1 mounted on long stalk 2 not as above

*70.	Tarsus I; position of famulus in relation to rhagidial organs	0 subtending, adjacent 1 subtending, separate 2 halfway up proximal 3 between proximal two 4 proximal to all 5 between second and third 6 distal to all 7 not as above
71.	Tibia I; position of proximal rhagidial organ	0 absent 1 on distal half of segment, in tandem 2 proximal and distal 3 parallel to distal organ, in separate pit 4 parallel to distal organ, in same pit
72.	Tibia I; famulus	0 absent 1 present
73.	Tibia I; form of other solenidia	0 absent 1 spiniform 2 erect
74.	Genu I; form of solenidia	0 absent 1 rhagidiform 2 spiniform 3 erect
75.	Tarsus II-IV; form of terminal setae	0 simple 1 capitate
76.	Tarsus II; famulus	0 absent 1 present
*77.	Tarsus II; form of famulus	0 simple 1 elaborately branched
*78.	Tarsus II; position of famulus	0 subtending rhagidial organs 1 halfway up proximal 2 proximal to all 3 between proximal two 4 other than above
79.	Tarsus II; arrangement of rhagidial organs	0 longitudinal, in tandem 1 longitudinal, staggered parallel 2 obliquely parallel 3 in tandem and parallel 4 in 'N' formation 5 other than above
*80.	Tibia II; position of rhagidial organs	0 absent 1 distal 2 distal and proximal
*81.	Tibia II; form of distal rhagidial organ	0 normal, exposed 1 reduced, subcuticular 2 much enlarged, exposed

82,	Tibia II; form of solenidia other than rhagidial organs	0 absent 1 spiniform 2 erect
83,	Genu II; form of solenidia	0 absent 1 rhagidiform 2 spiniform 3 erect
84,	Tibia III; form of solenidia	0 absent 1 rhagidiform 2 spiniform 3 erect
85,	Genu III; form of solenidia	0 absent 1 rhagidiform 2 spiniform 3 erect
86,	Tarsus IV; form of solenidia	0 absent 1 spiniform 2 erect
87,	Tibia IV; form of solenidia	0 absent 1 rhagidiform 2 spiniform 3 erect
*88,	Genu IV; form of solenidia	0 absent 1 rhagidiform 2 spiniform 3 erect
89,	Distal genual papilla;	0 absent 1 present
*90,	Femora IV; spines	0 absent 1 present

8.2.3 Interpretation of the results.

One of the principal aims of a phenetic analysis is to reduce the original data matrix to a number of clusters of OTUs which will form the basis of a classification. Not only does this present the data in a way more easy to absorb, but the definitions given to the clusters are also useful for subsequently trying to place specimens.

Although some workers have tried to define the term 'cluster' (Johnson 1967, Wallace & Boulter 1968), there seems to be no satisfactory definition that suits all situations and it tends to be an intuitive concept. Indeed Bonner (1964), presenting a very practical opinion, thought that the most important criterion in recognizing clusters and similarity is the judgement of the worker and that all that is required of the conclusions is that they are valuable to the investigator. This is in contrast to the attitude of Bock (1977) who states that

'Judgement of the usefulness of classification is not in terms of the systematists who construct them, but with respect to the other biologists who are dependant upon classifications as the foundation for their comparative studies and the formation of their generalizations'.

Similarly, McNeill (1975, 1979) emphasises the greater importance of the classification being a convenient framework for summarizing the range of diversity of the taxa. The content can then be more readily remembered and utilized by other workers. McNeill calls this aspect of hierarchical classification its structural value and gives a simple demonstration. A classification of 100 taxa of the same rank into either 100 sections of one taxon or a single section of 100 taxa would add nothing to the knowledge of the group.

In the present study, clusters were initially identified by searching the results of the analyses for large differences in percentage similarity (similarity matrices, minimum spanning tree), nesting hierarchies (single-linkage cluster analysis) and spatial isolation of OTUs (principal coordinates, of which plots of the two best axes only will be illustrated).

Having identified clusters, it is then necessary to decide at which point a particular taxon is delimited, *i.e.* which taxonomic rank should be assigned to the different clusters. As the present study is concerned with arranging the species of a single superfamily, the choice for the clusters will be between these two ranks. Again there are no hard and fast rules to apply but, in assigning rankings to the eupodoid taxa, guide-lines offered in Abbott *et al* (1985) and summarized as follows, were considered:

- a) to try to place taxa at ranks which have a comparable scale of discontinuities similar to that in the neighbouring taxa.
- b) to use the genus as the principal unit for information retrieval.

8.2.4 Runs of the analyses

Since the data matrix compiled for this study (75 OTUs and 90 characters) was too large to compute in a single analysis, a trial run (Run 1) was first carried out on the largest possible matrix of 70 OTUs and 60 characters (see Tables 5 & 6 for details).

The result of Run 1 showed two clearly separated groups of 38 and 32 OTUs (Figs 30, 31). When the omitted characters were compared for the two groups, it was evident that their inclusion would only reinforce this separation. Consequently, it was also possible to assign the five excluded OTUs to the correct group. It was, therefore, decided to run TAXON, using the complete data set, on the two groups separately (Runs 2 & 3), as this would maximise clustering within the two groups.

RUN 1

Similarity matrix

The computer refused to print out a similarity matrix as there were too many observations to be practically reproduced.

Principal co-ordinates (Figs 30)

The first three axes account for 60% of the total variation and so less than half of the remainder is obscured from view. The plots, therefore, give a reasonable visual overview of the groupings.

In the plot of the first two axes (accounting for 51% of the total variation), two large groups of OTUs separate out. Group 1 is located to the left of the plot and comprises the subgroups (a)-(j) delimited in the minimum spanning tree and single-linkage cluster analysis (see below). These represent the taxa conventionally classified in the families

Eupodidae, Penthaleidae and Penthalodidae. Group 2 contains subgroups (k)-(n) which represent the members of the families Rhagidiidae and Strandtmanniidae.

The two groups can be defined as follows. In members of group 1:

- adanal setae are absent;
- the chelicerae are weakly chelate;
- the palp genu is longer than broad;
- the adoral setae are minute;
- the external vertical setae are anterior to the trichobothria;
- the coxae are relatively indistinct and widely separated medially.

In the members of group 2, by contrast:

- adanal setae are present;
- the chelicerae are strongly chelate;
- the palp genu is approximately round;
- the adoral setae are long;
- the external vertical setae are level with the trichobothria;
- the coxae are well-defined and almost meet medially.
- the distal rhagidial organ of tibia II is subcuticular.

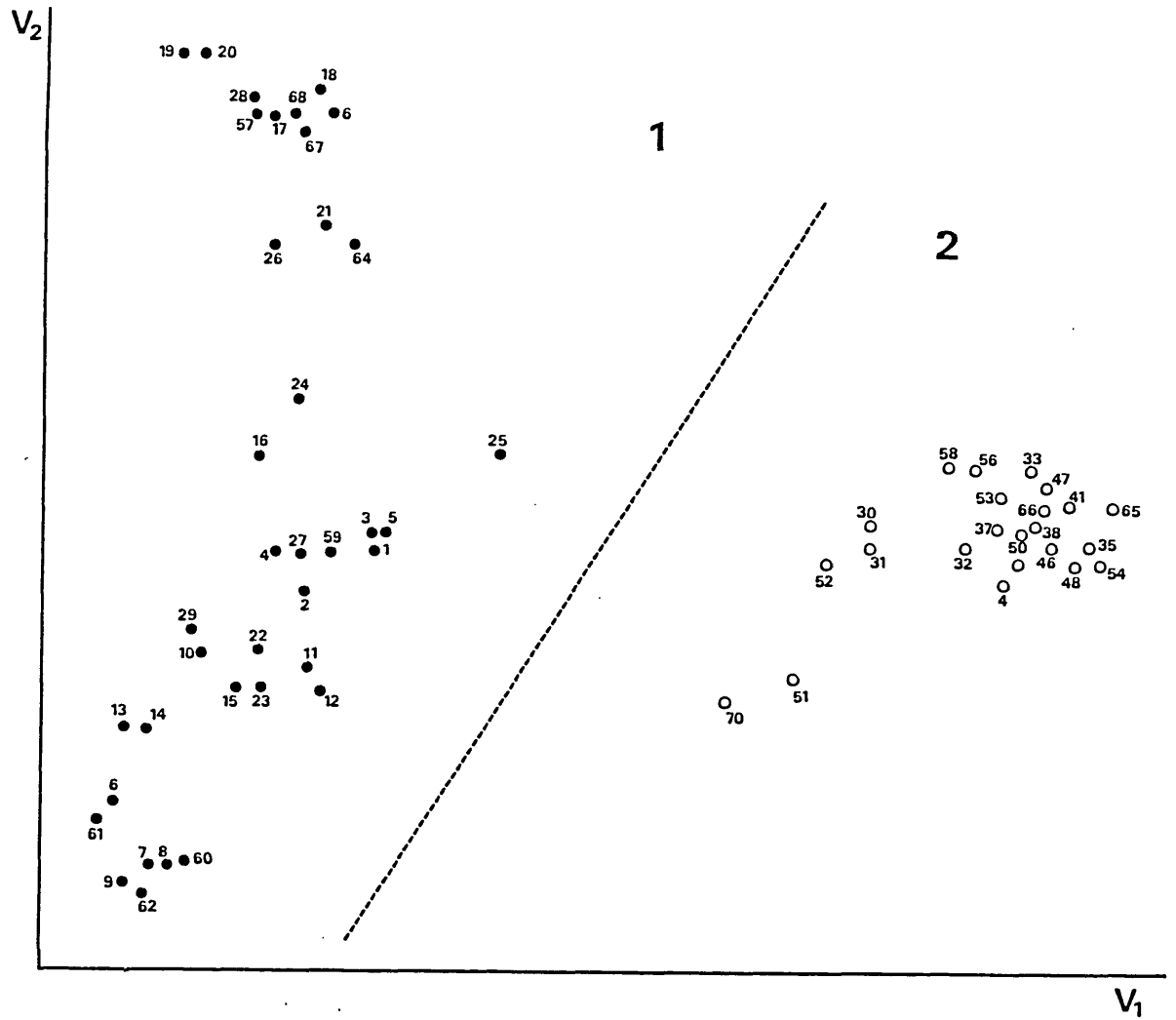


Fig. 30: Principal co-ordinates of the 70 OTUs included in Run 1 of the phenetic analysis. Groupings recognized comprise those species conventionally classified in the families Eupodidae, Penthaleidae and Penthalodidae (1) and Rhagidiidae (2).

Minimum spanning tree, single-linkage cluster analysis (Fig. 31) and nearest neighbours list (App. I)

In the minimum spanning tree (not shown), subgroupings indicated by OTUs linked by high percentage similarities are separated from other such OTUs by relatively low percentages. In the dendrogram of the single-linkage cluster analysis, these subgroupings are defined by a phenon-line drawn at 89% similarity. Referral to the nearest neighbours list confirms the coherence of these clusters, which are as follows:

- a) A small tight cluster is formed by the OTUs 1, 4 and 59 with 25 and 29 more loosely associated. Also attached to this cluster are OTUs 2, 5, 3 and 27.
- b) OTUs 22, 10, 15, 16 and 24 are loosely attached to each other.
- c) OTUs 11, 12 and 23 form a tight group.
- d) OTUs 13 and 14 form an isolated pair.
- e) Seven OTUs (6, 61, 62, 7, 8, 9 and 60) form a discrete group although there is a relatively low similarity of 93% separating off OTUs 6 and 61.
- f) OTUs 64 and 21 are paired together.
- g) OTUs 67, 57, 28, 68 and 69 form a fairly tight group.
- h) OTU 26 is widely separated from all others.
- i) OTUs 17 and 18 form an isolated pair.
- j) Another isolated pair is formed by OTUs 19 and 20.
- k) A large cloud of OTUs with no clear discontinuities comprising OTUs 32-50, 53-56, 58, 63, 65, 66.
- l) OTUs 70 and 51 are an isolated pair.
- m) OTUs 30 and 31 are also an isolated pair.
- n) OTU 52 is isolated.

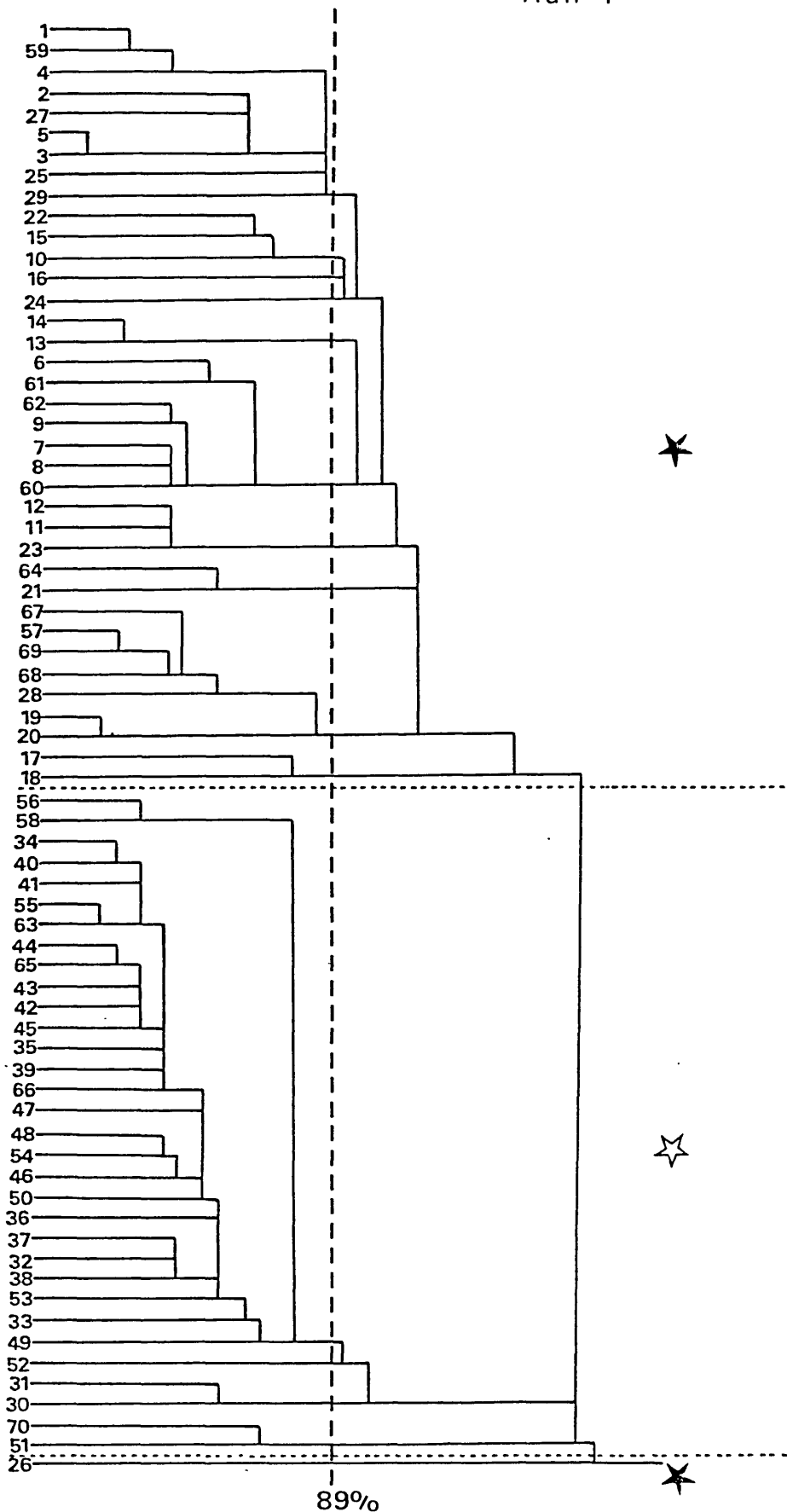


Fig. 31. Single-linkage cluster analysis of the 70 OTUs included in Run 1 of the phenetic analysis.

- - - - phenon, ★ group 1 OTUs, ☆ group 2 OTUs.

RUN 2

Characters chiefly influencing the formation of clusters fall into one of three categories. The first comprised those characters which were consistent within clusters and, although none was exclusive to any one, occurred in unique combinations. These are:

- the position of the internal vertical, external vertical and scapular setae and setae (C₇);
- the form of the palp tibiotarsus;
- the number of setae on coxae III and IV and of pseudanal setae;
- the form of the sejugal furrow and of femur IV.

The second type is those that are unique to the members of a single cluster, such as:

- expanded internal vertical setae or prodorsal trichobothria;
- opisthosomal segmentation and trichobothria.

Finally, the third category comprises those characters which are consistent within most but not all of the clusters, for example:

- the arrangement of the genital setae.
- the number of genital and aggenital setae;
- the length of leg I in proportion to the body;
- the number, form and arrangement of rhagidial organs.

Clusters indicating genera.

In the single-linkage cluster analysis (Fig. 32, p. 164), the generic phenon line was drawn most satisfactorily at 89% similarity. This position was supported by evidence from the minimum spanning tree (Fig. 33, p. 165) and the adapted similarity matrix (Fig. 34, p. 166). The clusters are described in the order in which they appear in the single-linkage cluster analysis, the OTU number of members being given in brackets after the species name.

The first three axes of principal co-ordinates account for 52% of the total variation, the first two for 43% (Fig. 35, p. 167), consequently, the plots were regarded as giving a reasonable visual representation of groupings.

Eupodes-group

Eupodes 1 (1), *Eupodes* 6 (32), *Eupodes alaskanensis*¹ (4) and *Eupodes* 3 (31) form a coherent cluster, the association being supported by the OTUs appearing in each others' nearest neighbours list (App. 2).

The members share the following character states:

- internal vertical setae located on the naso;
- filiform prodorsal trichobothria;
- setae (c_2) level with (c_1);
- long slender palp tibiotarsus;
- coxa III and IV with respectively four and three setae;
- (g_4) lateral to the other genital setae;

¹ In each section, names of species are given in full when first cited and then subsequently abbreviated.

three pairs of pseudanal setae;
 femur IV enlarged;
 tarsi I and II with two rhagidial organs;
 tibiae I and II with a proximal erect spine.

Benoinyssus-group

Associated with the *Eupodes* group, *E. momeni* (2), *Benoinyssus najae* (27) and *Eupodes ereynetoides* (5)¹ form a discrete cluster. They are unique amongst eupodoids in having opisthosomal setae (f_1) in the form of trichobothria. In addition, the external vertical setae are inserted approximately a fifth of the distance between the trichobothria and the anterior limit of the prodorsum, while the famulus of tibia I is absent.

This is a relatively heterogeneous group, the members differing in characters that will be seen to be constant in most others. *E. momeni* and *B. najae* have relatively longer internal vertical setae and a differently shaped naso than *E. ereynetoides*. The number of aggenital setae also varies; *E. momeni* has eight, *B. najae* 12 and *E. ereynetoides* 10. *E. ereynetoides* is unique in possessing bridge-like rhagidial organ on tarsi I and II, while the genital setae are arranged with (g_4) lateral and not in single file. The flexibility of polythetic groupings, however, allows this variability.

Since Fain (1958) diagnosed *Benoinyssus* by the presence of opisthosomal trichobothria, all the members of the cluster are included in this genus.

¹ When type material was made available to me, I discovered that *E. ereynetoides* (5) and *Eupodes 4* (3) were conspecific.

Eupodes angardi (25)

Associated with the above taxa, but delimited by the phenon as a monotypic 'genus', is *E. angardi*. It possesses no unique character and shares many of the attributes of the first group described, but differs most obviously by the slender femur IV and by the presence of an erect solenidion on genua I to III and on tibia IV. Despite these differences, *E. angardi* will fit the polythetic concept of the *Eupodes*-group, as it shares most but not all of the defining characters.

Egypteupodes strandtmanni (29)

The position of *E. strandtmanni* is similar to that of *E. angardi* but, by contrast, it possesses a character unique amongst eupodoids in that it lacks internal vertical setae. Examination of type material of this taxon, however, revealed that, contrary to details given in its description, the normal '*Eupodes*' arrangement of the genital setae and the complement of solenidia are present. Consequently, *E. strandtmanni* would be more aptly included in the *Eupodes*-group.

The following five taxa, though each delimited by the generic phenon, could all be accommodated in a single polythetic grouping:

1) *Eupodes 11* (22)

Eupodes 11 can be recognized by:

- the position of the scapular setae posterior to the trichobothria;
- the ovoid palp tibiotalar setae;
- the genital setae in single file;
- the three pairs of pseudanal setae;
- leg I being only two-thirds of the body length;

the slender femur IV;

tarsi and tibiae I and II all bear two rhagidial organs.

2) *Caleupodes reticulatus* (10)

C. reticulatus is another isolated OTU. It uniquely possesses external evidence of opisthosomal segmentation but, apart from this, the characters which have been used to define other generic clusters occur in unique combination in *C. reticulatus*. For example:

the internal vertical setae are located on the naso;

the palp tibiotalpus is slender;

the genital setae form a single file;

only two pairs of pseudanal setae are present;

tarsi and tibiae I and II all bear two rhagidial organs;

femur IV is slender.

3) *Eupodes 8* (15)

This taxon possesses two unusual character states - opisthosomal seta *f*₁ has a bothridial base, while coxa III bears only two setae. Other character states observed include:

the slender palp tibiotalpus;

the arrangement of the genital setae in single file;

two pairs of pseudanal setae;

leg I approximately three-quarters of the body length;

the slender femur IV;
 tarsi I and II with respectively two and three rhagidial organs;
 tibiae I and II with a proximal erect spine and a distal rhagidial organ.

4) *Eupodes 9* (16)

Eupodes 9 shares many character states with *Eupodes 8* but differs by possessing three pairs of pseudanal setae, three setae on coxa III, three rhagidial organs on tarsus II and two on tibiae I and II.

5) *Hawaiieupodes thermophilous* (24)

H. thermophilous can be characterized by the lack of both tarsal famuli. The prodorsal setae and leg solenidia are arranged as in the members of the *Eupodes*-group but *H. thermophilous* differs by possessing three setae on both coxae III and IV and genital setae in single file.

Cocceupodes-group

A well-defined cluster is formed by the seven species of *Cocceupodes* (OTUs 6, 34, 33, 7, 8, 35 and 9), each appearing in the others' nearest neighbour list. The members can immediately be recognized since the internal vertical setae are inserted posterior to the naso while unusually, though not uniquely, the apotele of leg I is often reduced. In addition, all the OTUs share the following character states:

an ovoid palp tibiotarsus;
 the sejugal furrow is represented by a narrow band of striae;
 setae (C₂) are located level with the trichobothria;
 the external vertical and scapular setae occupy an anterior position;
 both coxae III and IV support three setae;
 the genital setae are in single file;
 two pairs of pseudanal setae occur;

femur IV is enlarged;

solenidia other than rhagidial organs are absent.

Another unique feature, which occurs in only some of the members, is that subclavate and clavate internal vertical setae are present. In addition, there is some variation within this group in character states which in others appear to be constant. For example, the number of genital and aggenital setae and the arrangement of the rhagidial organs.

C. australis (6) and *C. breweri* (34) are somewhat isolated from the other *Cocceupodes* species by a relatively low percentage similarity in the minimum spanning tree and single-linkage cluster analysis, while they are spatially separated in principal co-ordinates plots. Apart from aspects of the arrangement of the rhagidial organs, however, there are no unifying characters to suggest that the cluster should be further divided.

Linopodes-group

Associated with the above cluster are the two *Linopodes* species (OTUs 13 and 14), which are characterized by the very long slender first legs, which are from four to six times body length. They possess an unusually narrow subcapitulum and slender chelicerae with weak short chela. They share many character states with the *Cocceupodes* species, but differ by having the fourth genital seta lateral to the others, a long slender palp tibiotalus and a slender femur IV.

Claveupodes-group

The three species of *Claveupodes* (OTUs 11, 12, 23) form a clear group delimited in all analyses. It can be immediately separated from other clusters by the presence of expanded prodorsal trichobothria, being subclavate or clavate. The members are also distinguished by other

characters such as the inconspicuous naso with the internal vertical setae inserted at its base, the eye-like form of the lyrifissures and the terminal anus. It is notable that these species are the smallest of eupodoids with the range in body length of 174-205 μ m.

Halotydeus-group

H. hydrodromus (21) and *H. signiensis* (36) occupy an isolated position in principal co-ordinates plots while, in the minimum spanning tree, they are separated from other taxa by a similarity of 82%. The 90% similarity between the two taxa is rather low compared with that found between members of other clusters but is apparently due to the influence of the difference in setal complements. The cluster can be adequately defined by the short robust palpal segments, the terminal anus and the presence of respectively three and two setae on coxae III and IV. The members also possess semi-erect rhagidial solenidia, erect solenidia on most of the leg segments and a distal papilla on the leg genua.

Stereotydeus-group

Another close association comprises the species classified in the genus *Stereotydeus* (OTUs 37, 39, 30, 40, 38 and 28). This is a heterogeneous group in some respects. For example, *S. villosus* (28) bears only three setae on coxa III instead of the four present in the other members, while *S. punctatus* (38) possesses a dorsal and not subterminal anus. The cluster can, however, be clearly distinguished since all members share the following features:

- an epirostrum;
- a sejugal furrow which does not clearly subdivide the idiosoma;
- two longitudinal opisthosomal furrows;

coxae with only the distal margins delimited;
rounded rectangular and clearly delimited genital shields;
erect solenidia on many of the leg segments;
a distal papilla on the leg genua;
lack supracoxal setae and the famulus of tibia I

Penthalodes-group

The isolated pair of *Penthalodes* species (OTUs 19 and 20) shares most of the character states described for the above cluster. However, it differs by lacking any external evidence of the sejugal furrow, the body is ornamented dorsally by a V- or Y-shaped indentation, cheliceral setae are absent and semi-erect solenidia occur on tarsi I and II.

Penthaleus-group

The two species of *Penthaleus* (OTUs 17 and 18) form an isolated group in all analyses. The relatively low level of 91% similarity to each other is attributed to the large differences in numbers of setae when, in fact, these two OTUs share a number of unifying character states. Apart from the neutrichous chaetome, they both possess short, robust palpal segments, distal genual papillae on the legs, erect solenidia on most of the leg segments and the fixed digit of the chelicerae terminating in a three-pronged process.

Linopenthaloides novazealandicus

The final cluster is represented by the isolated OTU *L. novazealandicus* (26) which has *H. signiensis* (36) as its nearest neighbour with the low similarity level of 72%. Again, this low value is likely to be due to the influence exerted by the high numbers of setae in the strongly

hypertrichous chaetome. *L. novazealandicus* possesses the unique character of having coxae II and III contiguous, rather than being widely separated. The marked neotrichy gives this species a general appearance like that of the two *Penthaleus* species, to which it has similarities of 70% and 68%. In principal co-ordinates, *L. novazealandicus* consistently appears in association with the two *Halotydeus* species. Despite the apparent similarity to *Penthaleus*, this OTU shares a greater number of character states with *Halotydeus*. These are the holotrichous prodorsum, the slightly forked fixed digit of the chelicerae and the terminal slit-like anus flanked by two flaps.

Run 2

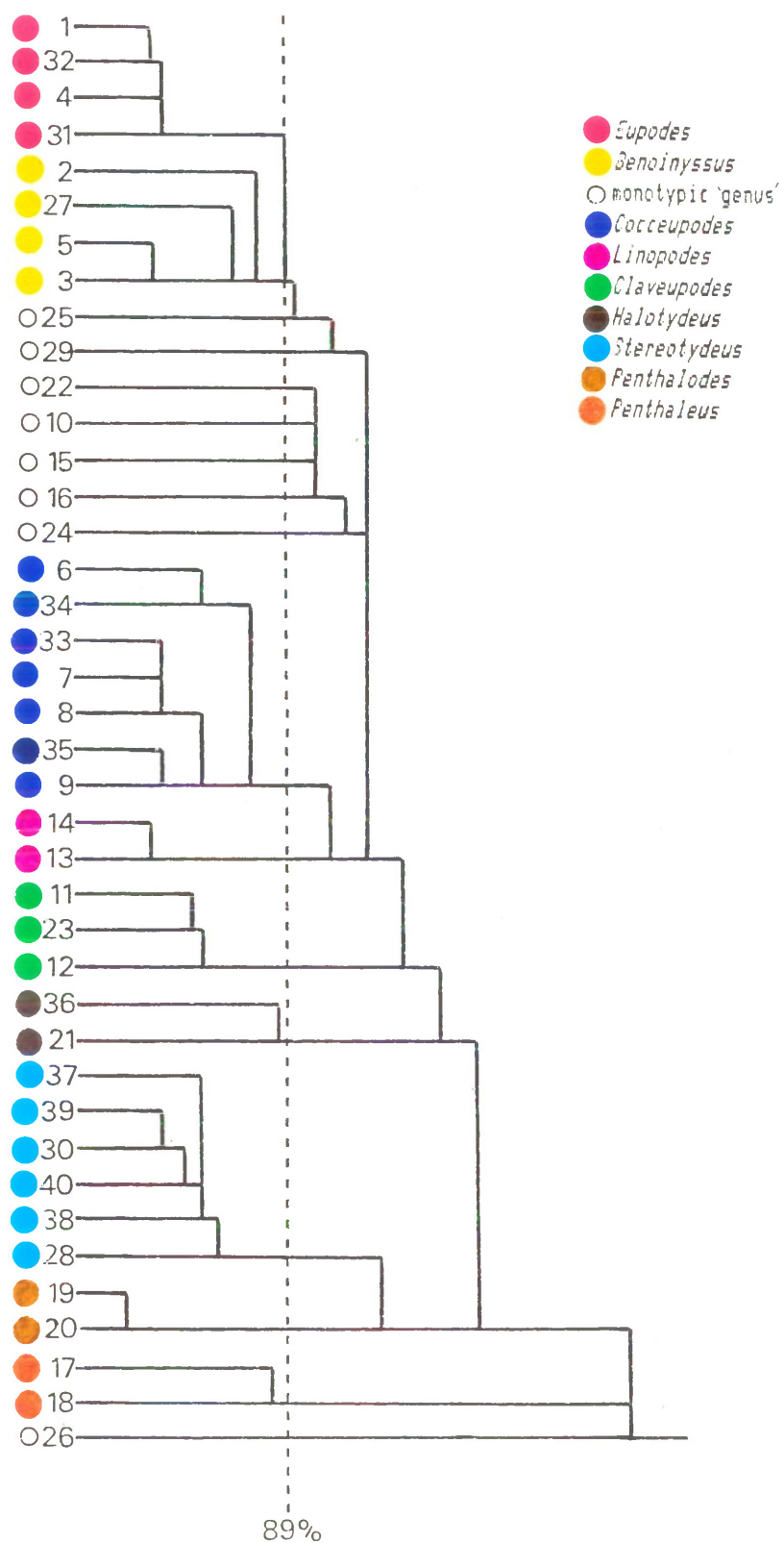


Fig. 32: Single-linkage cluster analysis of the 40 OTUs included in Run 2 of the phenetic analysis. Dotted line indicates generic phenon.

Run 2

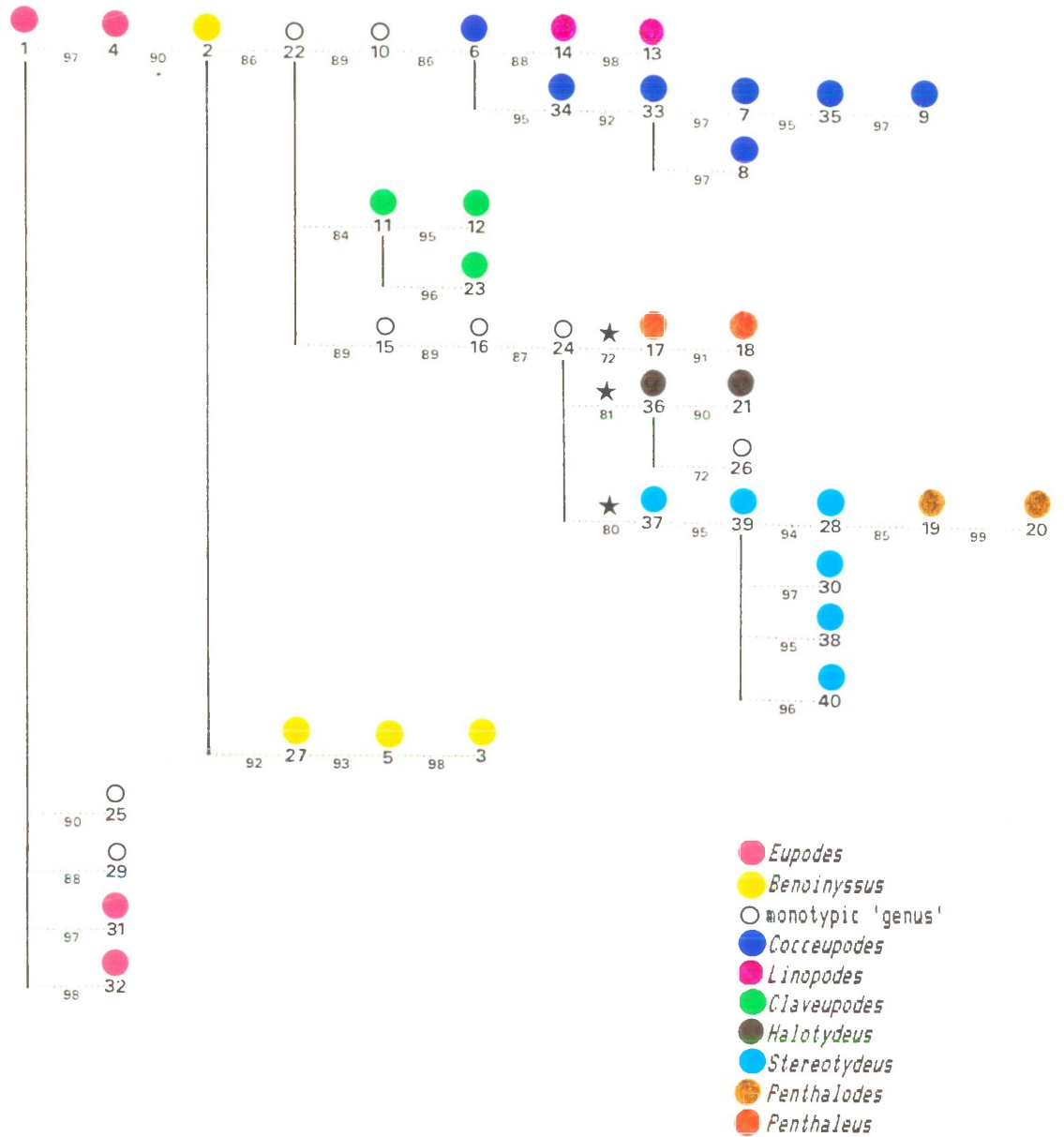


Fig. 33. Minimum spanning tree for the 40 OTUs included in Run 2 of the phenetic analysis. Numbers below dotted lines are percentages of overall similarity. ★ indicate particularly low values.

Run 2

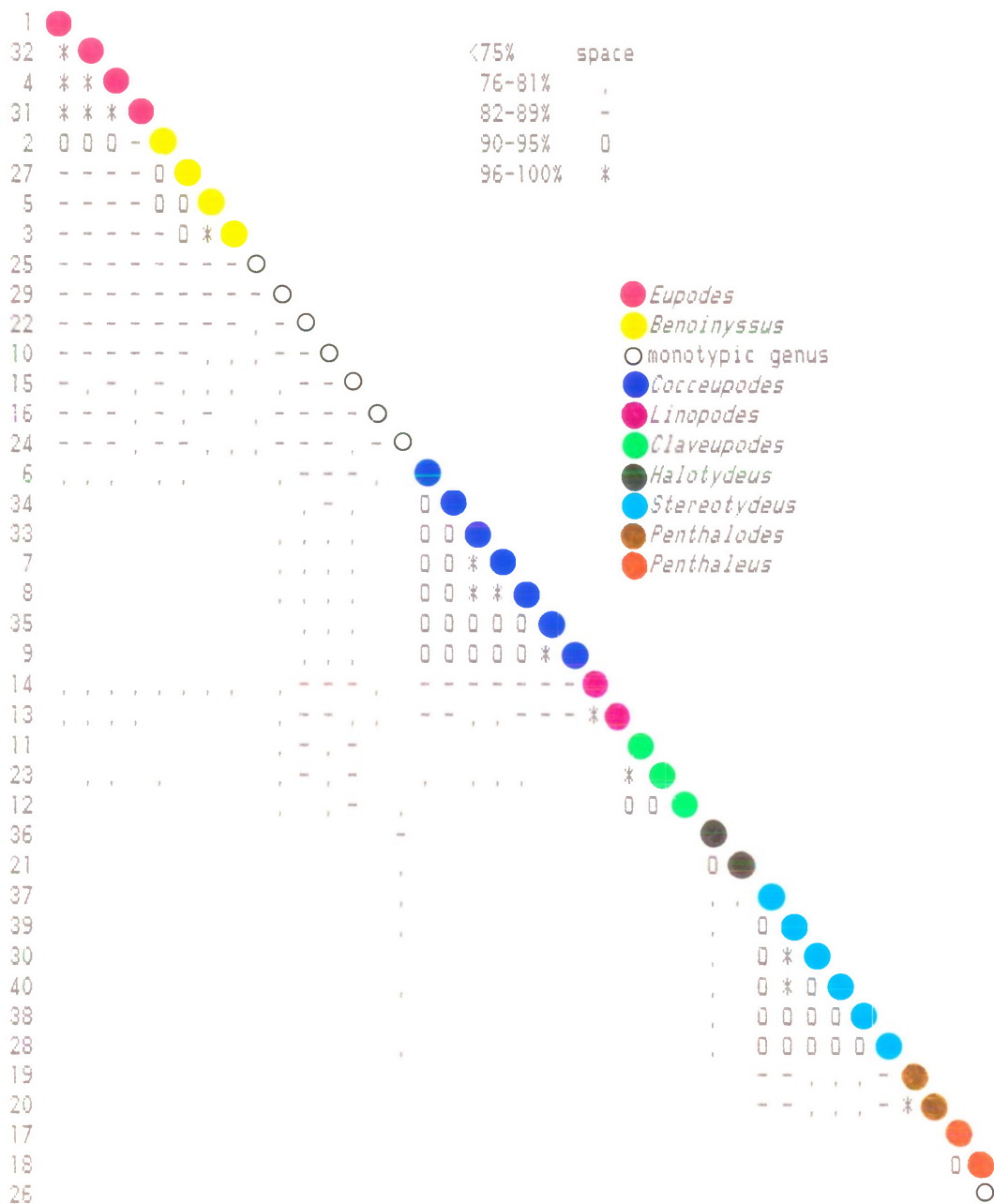


Fig. 34: Adapted similarity matrix for the 40 OTUs included in Run 2 of the phenetic analysis.

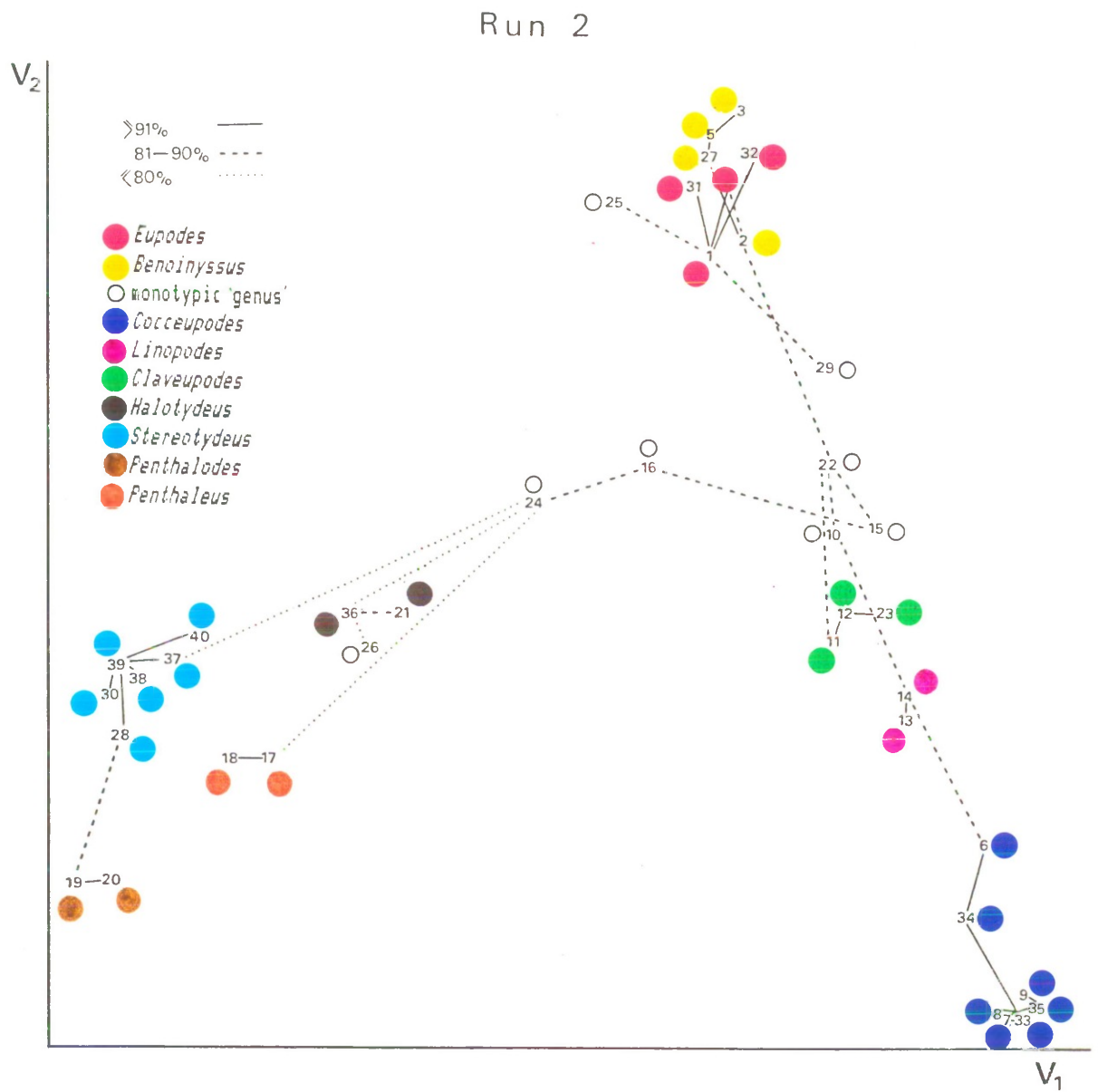


Fig. 35: Principal co-ordinates of the 40 OTUs included in Run 2 of the phenetic analysis. The linkages are taken from the minimum spanning tree and represent percentages of overall similarity as indicated.

Clusters indicating families

As a phenon line can be drawn to suggest the delimitation of genera, so can one be drawn to indicate families. Again, the priority in deciding at which level of similarity to do this is whether the groups so formed possess a set of unifying characters.

Amongst the high percentage similarities occurring in this study are some particularly low ones, noticeably those in the range 72% to 82% (Fig. 33). The most reasonable choices for drawing a family phenon line are at 80% or 73% similarity (Fig. 36). A phenon drawn at 80% divides the OTUs into four:

- 1) *Eupodes*-, *Benoinyssus*-, *Cocceupodes*-, *Linopodes*-, *Claveupodes*-, *Halotydeus*-groups; *E. angardi*; *E. strandtmannia*; *Eupodes 11*; *C. reticulatus*; *Eupodes 8 & 9*; *H. thermophilous*.
- 2) *Penthalodes*-, *Stereotydeus*-groups.
- 3) *Penthaleus*-group.
- 4) *L. novazealandicus*.

Drawing the phenon at 73% similarity divides the OTUs into three 'families'; 1) and 2) above are combined, whereas 3) and 4) are retained.

Neither of the above situations, however, is satisfactory. In both schemes, three clusters of OTUs, *Halotydeus*, *Penthaleus* and *Linopenthaloides*, which share a number of distinctive character states, are distributed amongst three familial clusters. Since the short robust palps, the more or less hypertrichous condition and the presence of erect solenidia on most of the leg segments distinguish the members of these groupings from all others, it would be nonsensical to separate them. As stated above, the separation of these taxa from each other is largely attributed to the strong influence imparted by the differences in setal counts which masks more important shared character states. Furthermore,

the merger of two very distinct groups of OTUs, (1) and (2), is unsatisfactory since the members of these two clusters are easily distinguished. The OTUs of (1) (excluding *Halotydeus*) possess the following character states:

- holotrichous chaetome;
- idiosomal furrows, if present, transverse
- reniform genital shields with indistinct outer margins;
- supracoxal setae present;
- coxae faintly but more or less completely delimited;
- two rhagidial organs on tarsus I.

The character states of the members of (2), on the other hand, are:

- chaetome usually neotrichous;
- epiprostrum present;
- raised prodorsal eyes;
- idiosomal furrows longitudinal, V- or Y-shaped;
- famulus of tibia I absent;
- genital shields rounded rectangular and clearly delimited from the surrounding integument;
- supracoxal setae absent;
- only distal margins of coxae delimited.

Run 2

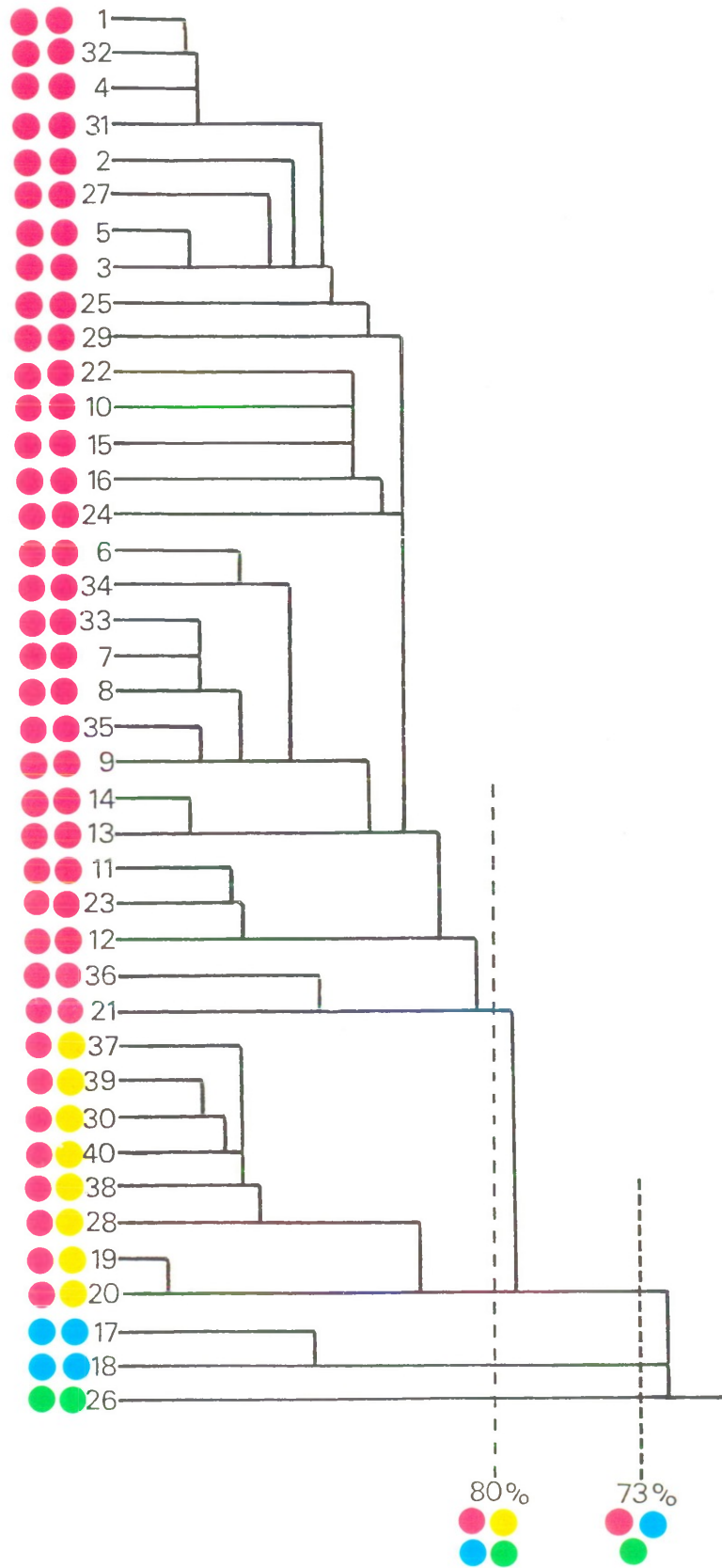


Fig. 36: Single linkage cluster analysis of 35 OTUs included in Run 3 of the phenetic analysis. Dotted lines indicate alternative familial phenons.

RUN 3

The OTUs in Group 2 did not fall into the number of more or less clearly separated clusters as did those of Group 1; the majority formed a cloud of points containing no major discontinuities. In such a situation, trends can be sought in the OTUs located at opposite extremes of the cloud and evidence sought from data not included in the original data set to support any groupings suggested.

The relative lack of clustering is not considered to be due to the different membership structure of the two groups - Group 2 comprised a larger number of genera represented by only one example, the type species. If these genera were valid, it would be expected that their representative OTU would still show a clear isolation in the various analyses.

Clusters suggesting genera.

In the principal co-ordinates analysis, the first three axes account for 43% of total variation, the first two for only 33%. Consequently, the visual representation could be regarded as rather unreliable. In practice, all plots presented a similar overall picture (see Fig. 37, p. 176), the majority of the OTUs lying in a diffuse cloud but with certain taxa being consistently separated.

In the dendrogram of the single-linkage cluster analysis (Fig. 38, p. 177), it is difficult to decide where to draw a generic phenon, while the percentage similarities in the minimum spanning tree show relatively little variation (Fig. 39, p. 178). A phenon drawn at 89% similarity delimits a large group of OTUs, corresponding to the diffuse cloud in

principal co-ordinates plots, and identifies the same isolates; this is reiterated in the adapted similarity matrix (Fig. 40, p. 179).

Coccorhagidia 1 (1) and *Hammenia macrostella* (2)¹ are separated from the main cloud by all three axes. These two are most obviously distinguished from other OTUs by the following character states:

palp tibiotarsus possesses heterogeneous setal forms and is markedly short;

only one pair of adoral setae is present;

distal rhagidial organ on tarsus I is an inverted U-shape;

the tarsal famuli are much enlarged and elaborately branched.

In addition, they possess a number of relatively uncommon, though not unique, character states. These are:

only cheliceral seta *cha* is present;

genu I has a rhagidial organ instead of the usual spiniform solenidion;

leg I is only about two-thirds of the body length;

the trichobothria are clavate;

the naso is indistinct;

the idiosomal length is at the small end of the size range (respectively 266 μ m and 284 μ m).

Brevipalpia minima (17) and the pair comprising *Pilorhagidia hirsuta* (27) and *Strandtmannia celtarum* (28) are at a similar level on axis 2 but well-removed from the remaining OTUs, while they are clearly separated from each other by axis 1.

¹ When type material was made available to me, I found *Coccorhagidia 1* and *Hammenia macrostella* to be conspecific.

B. mimima is unique in that the famulus of tarsus I is located halfway along the proximal rhagidial organ. Other, uncommon, character states are:

its small size (body length 355 μ m);

the short leg I (only just over half body length);

clavate trichobothria;

an inconspicuous naso;

nine and one setae occur respectively on the palp tibiotarsus and genu;

cheliceral seta *chb* is inserted in a depression;

the rhagidial organs on tarsus II are longitudinal and in tandem;

tarsus II lacks the famulus.

P. hirsuta (56) and *S. celtarum* (58) are unique amongst group 2 OTUs in being strongly hypertrichous and by possessing a tapering palp tibiotarsus. In addition, they possess clavate or subclavate trichobothria, nine setae on the palp tarsus and one on the palp genu.

Shibaia longisensilla (22) and *S. tatica* (35) can immediately be distinguished from other OTUs by the tarsal rhagidial organs being arranged in parallel and longitudinally along the segment, famulus I has an elongate stem and is distal to the rhagidial organs while, instead of having spiniform solenidia on other leg segments, they possess rhagidial organs. In addition, they are unusual in having only one cheliceral seta and four setae on coxa III.

The OTUs *Latoempodia macroempodiata* (3), *Thoria brevisensilla* (23) and the pair *Crassocheles muralis* (8) and *Parallelorhagidia evansi* (9) are delimited by the 89% phenon but only slightly separated along the principal co-ordinates axes. The first of these, *L. macroempodiata*, can be readily distinguished by the elaborate apotele of leg I. Other character states possessed include coxa III with four setae, nine setae on

the palp tibiotalpus while leg I is only about two-thirds of the body length.

The pairing of *C. muralis* and *P. evansi* is suspect. Despite sharing uncommon character states, such as nine palp tarsal setae and leg I shorter than the body, they differ as *P. evansi* has clavate trichobothria, whereas in *C. muralis* they are filiform.

Apotele I of *Thoria brevisensilla* (23) is larger than normal, though not on the scale of that of *L. macroempodiata*. It also possesses several of the uncommon character states, such as only one cheliceral seta being present, leg I is shorter than the body while coxa III supports four setae.

Within the cloud of the remaining 24 OTUs, groupings suggested by slight separation in principal co-ordinates plots and by a phenon drawn at 93% similarity are as follows:

- a) *Rhagidia punkva* (6)
- b) *Foveacheles* (*F.*) *osloensis* (15), *F. (Hirschmannetta) magna* (32), *Poecilophysis (Soprocheles) arena* (12), *Troglocheles strasseri* (13), *F. (Proxistella) terricola* (34), *Rhagidia (Austrorhagidia) mildredi* (5), *Poecilophysis (Procerocheles) spelaea* (26), *F. (Mediostella) rupestris* (29), *P. (F.) kerguelensis* (11), *Flabellorhagidia pecki* (14), *F. (Usitorhagidia) clavicrinita* (30), *F. (Propiorhagidia) mira* (31), *F. (Ternirhagidia) emendata* (33).
- c) *Elliotta howarthi* (10)
- d) *Robustocheles* (*R.*) *montana* (7)
- e) *Coccorhagidia clavifrons* (16)
- f) *Traegaardia dalmatina* (18)
- g) *Arctorhagidia mariehammerae* (19), *A. sateri* (25)
- h) *Eskimaia capitata* (20)

- i) *R. (R.) gelida* (4)
- j) *Evadorhagidia oblikensis* (21)
- k) *Tuberostoma gressitti* (24)

Attempts to define these clusters resulted in unsatisfactory, overlapping diagnoses, while referral to both species and characters that were not included in the original data matrix did not aid their clarification.

Clusters indicating families

No familial divisions could be recognized, the character states which did cause isolation of certain of the OTUs having been considered suitable for generic and not familial definitions

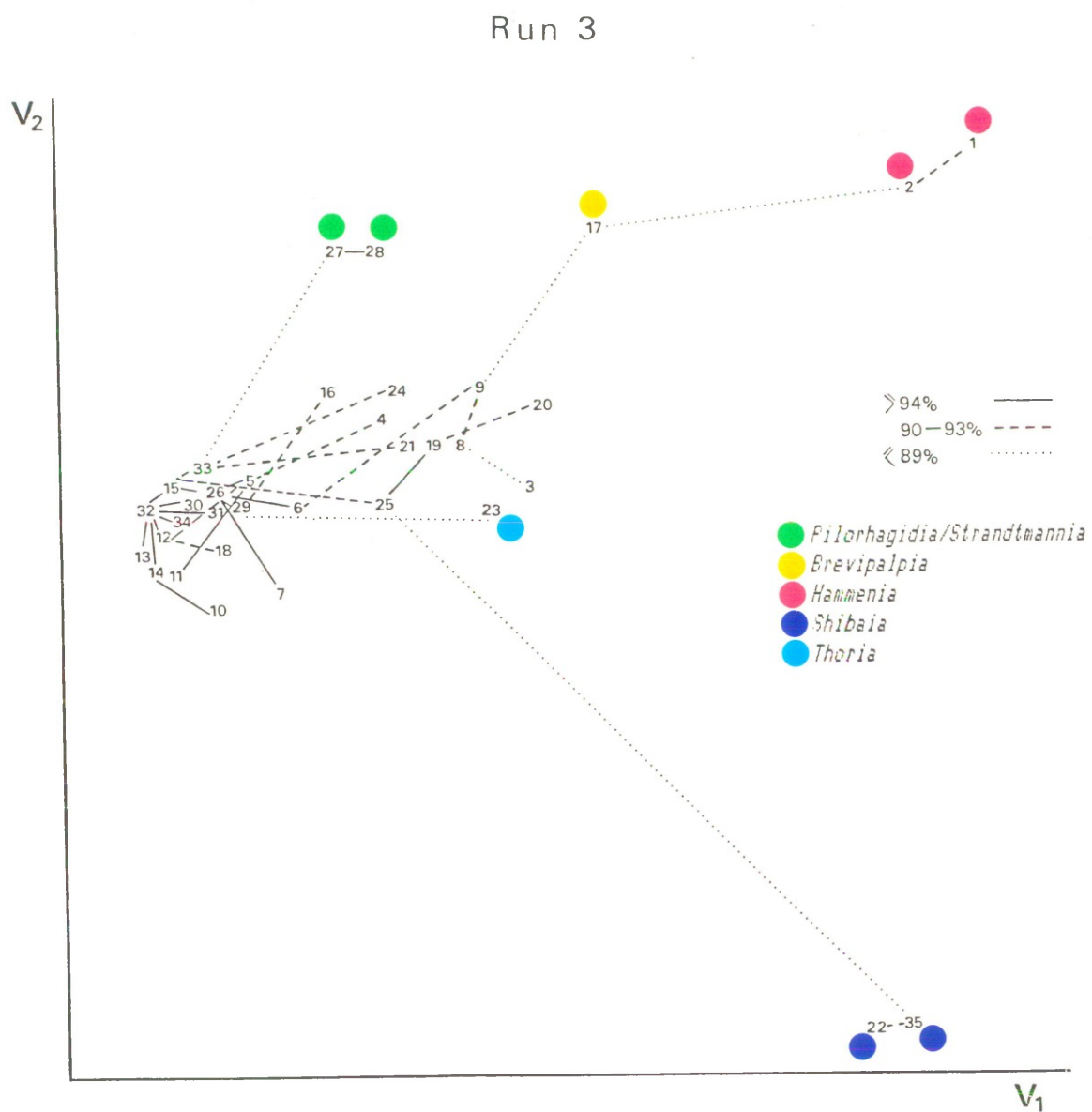


Fig. 37: Principal co-ordinates of the 35 OTUs included in Run 3 of the phenetic analysis. The linkages are taken from the minimum spanning tree and represent percentages of overall similarity as indicated.

Run 3

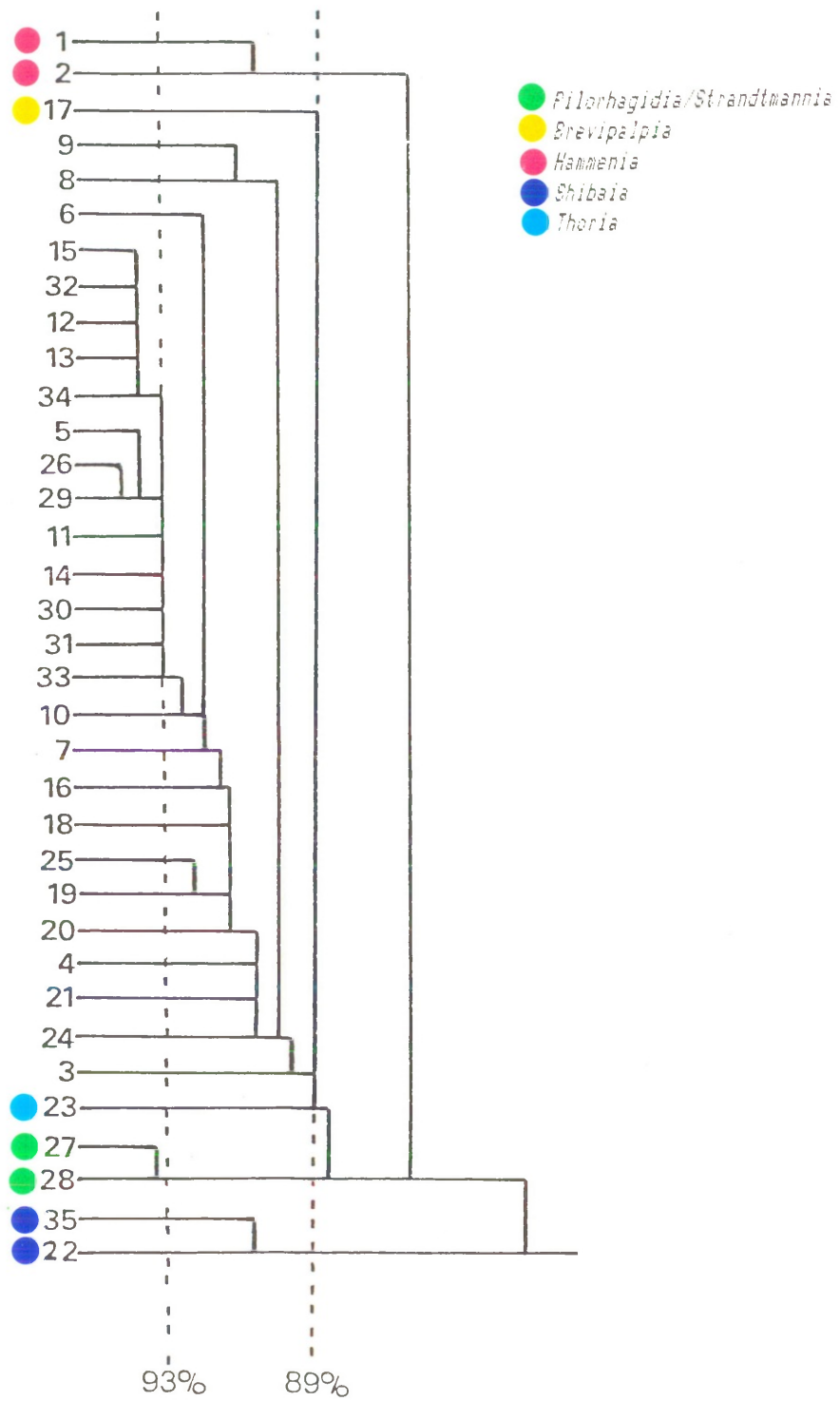


Fig. 38: Single linkage cluster analysis of the 35 OTUs included in Run 3 of the phenetic analysis. Dotted lines indicate alternative generic phenons.

Run 3

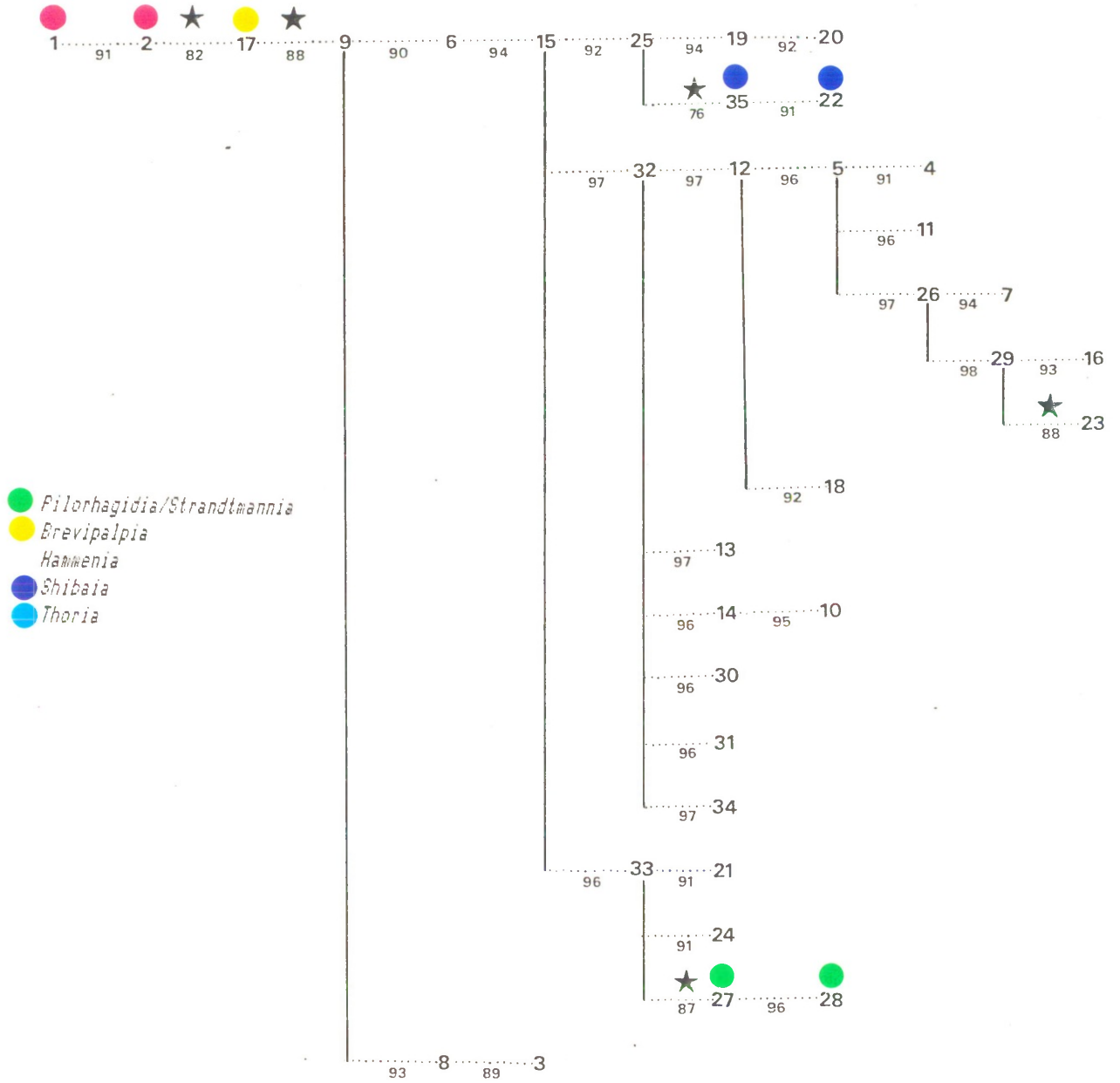


Fig. 39: Minimum spanning tree for the 35 OTUs included in Run 3 of the phenetic analysis. Numbers below the dotted lines are percentages of overall similarity. ★ indicate particularly low values.

Run 3

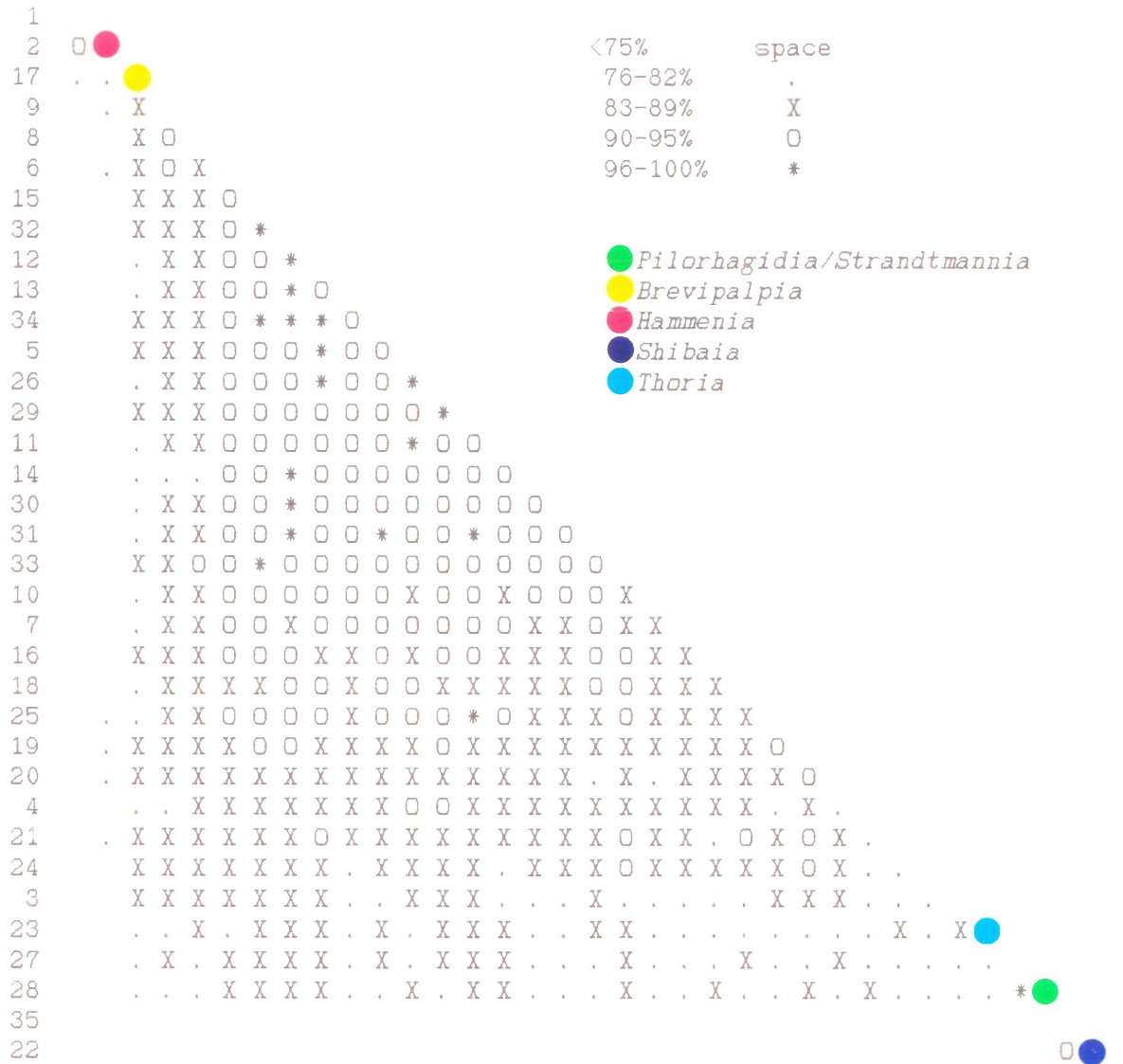


Fig. 40: Adapted similarity matrix for the 35 OTUs included in Run 3 of the phenetic analysis.

8.2.5 Survey (See section 8.4 for a full discussion)

Certain divisions of the Eupodoidea are demonstrated by the analyses described. The first run clearly divides the superfamily into a eupodid/penthaleid/penthalodid group and a rhagidiid/strandtmanniid group. Analysis of the first of the two caused the taxa to form a number of clearly separated clusters which can be adequately defined and are given generic status. Other OTUs were isolated and were treated either as monotypic genera or as members of a polythetic grouping. The definition of families in this group was not satisfactorily resolved by the analyses since the influence exerted by large differences in quantitative characters overshadowed more useful taxonomic features. With hindsight, the use of minima and maxima, rather than raw numbers, might have prevented some of this distortion.

The majority of the members of the rhagidiid/strandtmanniid group formed a diffuse cloud of points in principal co-ordinates analyses, while 'genera' indicated in single-linkage cluster analyses did not form diagnosable groups. This situation suggests that important taxonomic characters are being obscured and/or that the data set chosen was unsuitable. Character states vary much more widely in these taxa and occur in many more combinations than in the eupodid/penthaleid/penthalodid group, so resulting in the relative absence of clustering.

There are many more phenetic techniques available than those applied here to the Eupodoidea (see Sneath & Sokal 1973, Abbott *et al* 1985) and a criticism of lack of sophistication could be made. The methods chosen here, however, have been widely utilized by taxonomists and it is believed their use has been a valid trial of phenetic analysis.

omic analyses.
 on /redescriptions.

- + *Crassocheles muralis*
- + *Parallelorhagidia evansi*
- + *Elliotta howarthi*
 - *Poecilophysis (P.) kerguelensis*
- + *P. (Soprocheles) arena*
 - *Troglocheles strasseri*
- + *Flabellorhagidia pecki*
 - *Foveacheles (F.) osloensis*
- + *Coccorhagidia clavifrons*
- + *Brevipalpia minima*
 - *Traegardhia dalmatina*
 - *Arctorhagidia mariehammerae*
 - *Eskimaia capitata*
 - *Evadorhagidia oblikensis*
 - *Shibaia longisensilla*
 - *Thoria brevisensilla*
 - *Tuberostoma gressitti*
 - *Arctorhagidia sateri*
 - *Poecilophysis (Procerocheles) spelaea*
 - *Pilorhagidia hirsuta*
 - *Stereotydeus nudisetatus*
 - *Strandtmannia celtarum*
- Eupodes 3*
- Eupodes 6*
- Cocceupodes paradoxus*
- + *Cocceupodes breweri*
- + *Cocceupodes stellatus*
 - *Foveacheles (Mediostella) rupestris*
 - + *F. (Usitorhagidia) clavicornita*
 - *Halotydeus signiensis*
 - *Foveacheles (Propriorhagidia) mira*
 - *F. (Hirschmannetta) magna*
 - *F. (Ternirhagidia) emendata*
 - *F. (Proxistella) terricola*
 - *Stereotydeus shoupi*
 - Stereotydeus punctatus*
 - Stereotydeus meyeri*
 - Stereotydeus delicatus*
 - Shibaia tatrca*

8.3 CLADISTIC ANALYSIS

The cladistic method was devised by the German entomologist Willi Hennig and detailed in his book *Grundzüge einer Theorie der Phylogenetischen Systematik* (1950), the English translation of which was published in 1966. The method attracted a lot of interest and has subsequently been adapted by other workers to the extent that some of their modifications no longer agree with the basic concepts of Hennig.

There are many accounts describing the cladistic method (see for example, Eldredge & Cracraft 1980, Patterson 1980, Arnold 1981, Nelson & Platnick 1981, Wiley 1981, Patterson 1982, Humphries & Funk 1984) and so the following account only serves to provide the basic concepts.

Principles of cladistics

The central aim of a cladistic analysis is to group taxa into holophyletic units, *i.e.* those comprising all and only the descendants of a common ancestor, on the basis of shared derived characters (synapomorphies). The term 'holophyletic' is preferred to 'monophyletic' since the latter is traditionally used for a group of taxa comprising a single known or inferred ancestral species and some or all of its descendants. Shared primitive characters (symplesiomorphies) make no contribution to the arrangement of taxa. This conclusion obtains from Hennig's observation that plesiomorphic character states tend to be retained sporadically and so their use for indicating holophyletic groupings of taxa only occurs at the hierarchical level at which they first arise, *i.e.* are apomorphic. Neither paraphyletic (a group of taxa comprising a single known or inferred ancestral species and some but not all of its descendants) nor polyphyletic (a group of taxa that does not include the most recent known or inferred common ancestor of all the

taxa) groupings are recognized as valid by cladists since they cannot be defined by synapomorphies.

Having chosen the taxa for study, the next step is to identify plesiomorphic and apomorphic character states. In addition, if a character has more than two states, the direction of the change, its polarity, from the plesiomorphic to the apomorphic must be established. The resulting sequence of character states is termed a transformation series. Generally, the more complex a character becomes, the more apomorphic it is thought to be but a number of procedures for recognizing apomorphies have been suggested:

1. Common equals primitive. The assumption that a character state occurring frequently in a group must be primitive (Estabrook 1977) is generally regarded to be misleading and inaccurate (Watrous & Wheeler 1981) since the incidence of a particular character state in the majority of the taxa under study does not preclude it from also being found in closely related groups.

2. Ontogeny. Two laws concerning ontogenetic development are utilized. Haeckelian recapitulation ('ontogeny recapitulates phylogeny') states that the ontogenetic development of an organism traces the sequence of its adult ancestors, so revealing plesiomorphic character states. Secondly, three of von Baer's laws are relevant to the analysis of synapomorphies:

- (1) during ontogeny, general characters appear before the special ones;
- (2) less general and then special characters develop from the more general ones;
- (3) during an organism's development, it becomes progressively more different from others.

Although both concepts have proved useful in analyses, the occurrence of neotenuous organisms limits their effectiveness.

3. Palaeontology. It is considered that palaeontological evidence will reveal possible ancestral-descendant lines of taxa and hence plesiomorphic-apomorphic sequences of characters, *i.e.* transformation series. To do this, however, it would be necessary to know the complete palaeontological record, while it is not necessarily true that characters occurring early in the fossil record are primitive.

4. Out-group comparison. This is the most commonly used and reliable method. The group under study is compared with an out-group which ideally is its nearest relative, *i.e.* its sister-group. Thus, in a group of three taxa in which a character has one state in two and another in the third, that state which does not occur in the out-group is considered to be apomorphic (Fig. 41A).

Two aspects cause difficulties in this method, if the character states of the study group are absent from the out-group and if a sister-group cannot be identified. The former can be resolved by using a wider sample of related taxa so that, if a character state found in the study group and absent in the sister-group occurs in the wider group, it is considered to be plesiomorphic (Fig. 41B).

In the absence of an identifiable sister-group, an out-group comprising a number of potential sister-groups, none of which share a derived character with the study group, may be used. If all of these groups possess a character state which also occurs in the study group, it is assumed to be plesiomorphic (Fig. 41C). Alternatively, a 'functional out-group' as described by Watrous & Wheeler (1981) can be used. Here, holophyletic groups identifiable within the taxon under study are used as out-groups of one another (Fig. 41D).

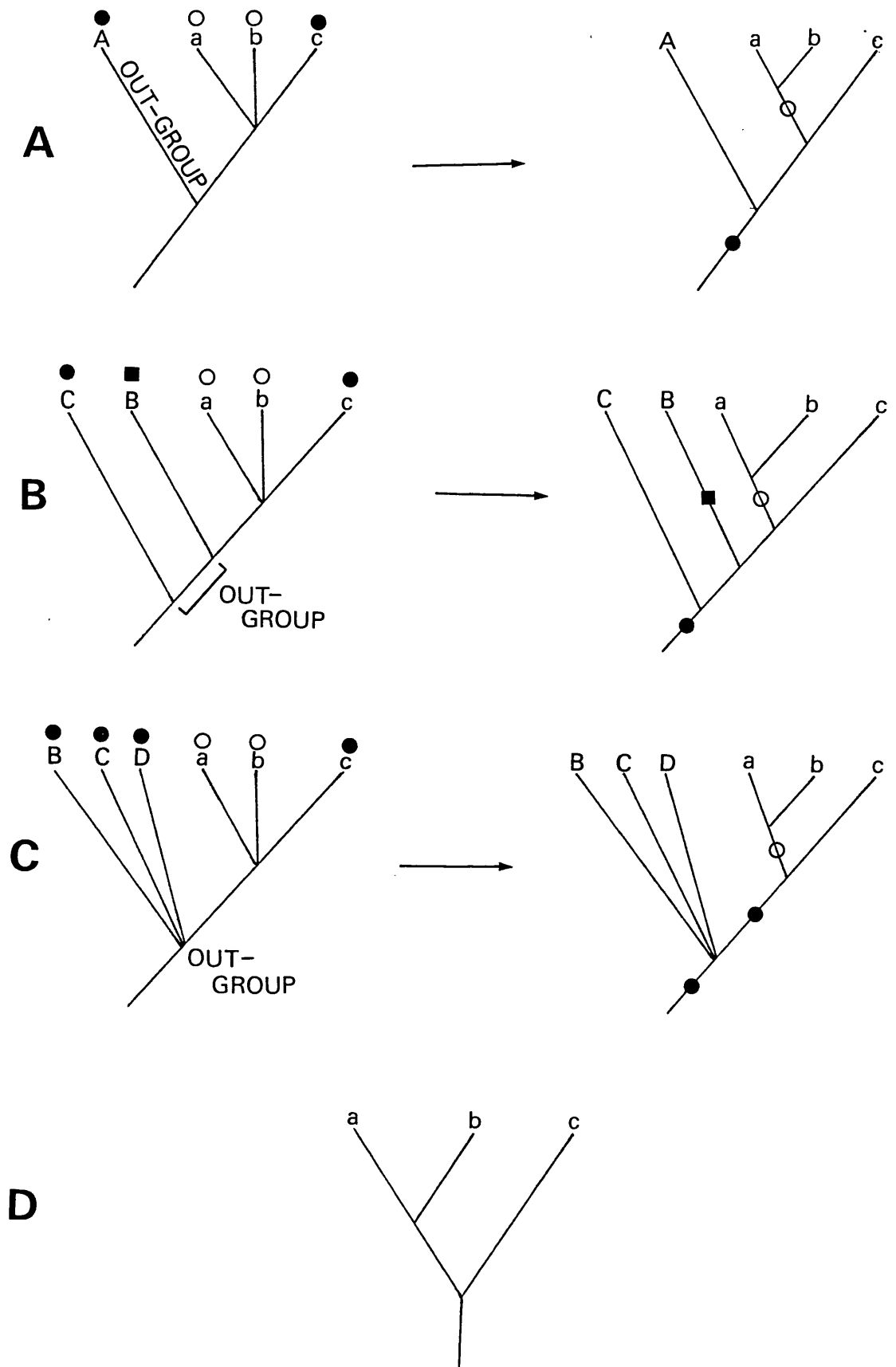


Fig. 41. Methods of out-group comparison (see text for explanation).

Having identified plesiomorphic and apomorphic states and the polarity of character change in the study group, the data matrix is searched for nesting sets of apomorphies. The result of a cladistic analysis is expressed in a cladogram (each holophyletic group in the cladogram being a clade), a branching diagram reflecting the hierarchical relationships of the taxa. The ends of the branches are occupied by the taxa, while the points at which branching occurs, the nodes, indicate apomorphic characters. For even a moderately-sized data matrix there are many possible combinations of characters and, therefore, alternative trees. Consequently, it is necessary to identify reversals, a character state which returns to its primitive condition and homoplasies. The latter comprises convergence, where resemblance occurs in non-homologous characters, and parallelisms, where the same character appears more than once independently. If conflicts in character analysis occur, the concept of parsimony is used to choose the 'best' cladogram whereby the tree which can be explained by the least number of homoplasies and reversals and the greatest number of congruent, i.e. corresponding, apomorphies is regarded as the 'best' tree. This is based on the assumption that evolution proceeds in the simplest, the most parsimonious, way. The great advantage that cladists attribute to their method over others is that it can be tested by the concepts of parsimony and apomorphy.

Initially, cladograms were considered to reflect the phylogenies of the taxa (for example, Eldredge & Cracraft 1980, Wiley 1981). However, more recently, certain workers (Platnick 1979, Patterson 1980, 1982, Nelson & Platnick 1981) disagree and regard cladograms merely to show the distribution of apomorphic characters. These workers form the school of cladistics known as transformed cladistics.

According to different opinions, the loss of a character can be treated as either an apomorphy or a plesiomorphy. The rationale for the former view assumes that the particular feature was originally present and so the loss of it also counts as an evolutionary novelty. The case for treating absence as a plesiomorphy is that it is a non-specific character which could be attributed to many organisms with no relation to the group being analysed.

Character weighting

Authors such as Eldredge and Cracraft (1980) believe that all hypotheses of synapomorphy are valuable for the evaluation of alternative cladograms and to be relevant for defining holophyletic groups at some level. Other workers, however, consider some synapomorphies to be more important than others and so should receive more weight (Hecht & Edwards 1976, 1977). Hecht & Edwards (1977) devised a system of weighting in the following order of increasing reliability:

- 1) states involving loss of a structure;
- 2) simplification of complex structures;
- 3) states resulting from changes in growth and developmental processes dependant on size, age and hormonal and other physiological relationships, e.g. characters related to allometric functions;
- 4) states that are largely integrated functionally and are subject to directional selection;
- 5) innovatively unique states.

Cladograms and classifications

A number of methods have been developed for converting cladograms to classifications (see Wiley (1981) for review). For example, Hennig (1969) and Løvtrup (1977) both devised a system which gave a unique numerical prefix to each taxon to indicate its position relative to the other. Although Løvtrup's system was less elaborate than Hennig's, both have the disadvantage of being difficult to memorize.

Over a number of years and acquiring a variety of names, a system has been devised which has gained general acceptance. It is commonly referred to as phyletic sequencing and Wiley (1979) describes in detail his version, the 'Annotated Linnaean hierarchy'. The principle of this method is that holophyletic taxa are listed with sister-groups given equal rank and within the same taxon of immediately higher rank. The various levels are indicated in the layout of the classification by indenting the different taxa by relative amounts. Sister-groups have the same level of indentation, while lower taxonomic ranks are indented beneath the higher taxa to which they belong. This system means that all the information in a cladogram can be conveyed in the classification and so can be redrawn from it.

The conventions of this system state that the resulting classification can contain the minimum number of redundant ranks, *i.e.* those that contain exactly the same members as the higher taxon that it belongs to, and that, wherever possible, natural taxa of essential importance to the group being classified should be retained at their traditional ranks.

A potential difficulty arises when a polychotomy occurs in a cladogram since this infers that interrelationships are not resolved. Nelson & Platnick (1981), however, also attribute their occurrence to a

minimum number of redundant ranks, i.e. those that contain exactly the same members as the higher taxon that it belongs to, and that, wherever possible, natural taxa of essential importance to the group being classified should be retained at their traditional ranks.

A potential difficulty arises when a polychotomy occurs in a cladogram since this infers that interrelationships are not resolved, although Nelson & Platnick (1981) also attribute their occurrence to vicariance events, i.e. when taxa split as the result of the development of a natural biogeographic barrier. Wiley (1979) stresses the importance of distinguishing polychotomies from a series of dichotomies and solves the problem by suffixing the taxon involved with '*sedis mutabilis*' (= changeable position). Thus the sequencing convention is maintained but it is immediately obvious that interrelationships are unresolved.

8.3.1 Cladistic analysis of the Eupodoidea

The taxa

The taxa included in the analysis are those listed in Table 6 plus the British eupodid species, *Eupodes* 13, which was found after completion of the phenetic study.

Character analysis

Not all of the characters used in the phenetic study were included for the cladistic analysis, primarily because homology could not be established with certainty. Some recoding of character states was necessary, the final list is given in Table 7. In the text, numbers given in brackets after characters are their references in the character list and on cladograms. Detailed descriptions and illustrations of character

states can be found in the account of external morphology (section 7.3) and in the descriptions of the taxa (section 10).

In common with other cladistic analyses of mites (Antony & Johnston 1984, O'Connor 1984, 1984a, Niedbala 1986), the determination of character state polarity in the Eupodoidea is made difficult by the lack of an established sister-group for out-group comparison. The sister-group of the Eupodoidea was sought from amongst the other members of the cohort Eupodina, namely the superfamilies Tydeoidea, Bdelloidea and Halacaroidea. Analysis of the cohort suggested the Tydeoidea, with the presence of four pairs of lyrifissures (1), a total of four pairs of setae on the subcapitulum (2), a solenidion on the palp tibiotarsus (3), linear palps (4) and a famulus on tarsus I (6) as synapomorphies (Fig. 42). The Tydeoidea, itself, was defined as a holophyletic group by the presence of fused chelicerae (5).

Using the characters resolved in an out-group comparison with the Tydeoidea, it was possible to establish the Eupodoidea as a holophyletic group and to further divide it into four holophyletic groups (Fig. 42). Although the Tydeoidea are proposed as the sister-group of the Eupodoidea, its derivative form means that some states found in the Eupodoidea do not occur in the Tydeoidea, hence the polarity of all the characters could not be established. These character states were therefore resolved by the method of using 'functional out-groups' as described by Watrous & Wheeler (1981). Thus, the holophyletic group comprising the families Eupodidae, Penthaleidae and Penthalodidae (see below) were used as the out-group for the Rhagidiidae, that comprising the Penthalodidae and Penthaleidae for the Eupodidae and the Penthaleidae and Penthalodidae acted as the out-group to each other.

Table 7. Character polarizations used in cladistic analysis

Out-groups used to determine polarity: (C) Cohort Eupodina; (T) Tydeoidea;
(F) Functional out-group

<u>Character</u>	<u>Plesiomorphy</u>	<u>Apomorphy</u>
1, Lyrifissures; four pairs (C)	absent	present
2, Adoral & subcapitular setae; total number of pairs (C)	more than four	four
3, Palp tibiotarsus; solenidion (C)	absent	present
4, Palps; form (C)	raptorial	linear
5, Chelicerae (C)	separate	fused
6, Tarsus I; famulus (C)	absent	present
6a, Tarsus I; form of famulus (T)	spiniform	stellate
7, Tarsus II; famulus (T)	absent	present
8, Naso (T)	absent	present
9, Palp genu; number of setae (T)	two	.1 one .2 three
10, Palp femur; number of setae (T)	two	.1 one .2 three
11, Tarsus I; solenidial form (T)	erect	recessed
12, Chelicera; form fixed digit (T)	weakly hooked	.1 terminates in 3 processes .2 strongly hooked
12a, Weakly chelate chela; form (F)	normal	reduced
13, Chelicerae; number of setae (F)	one	.1 nil .2 two
14, Trochanter III; number of setae (T)	one	.1 two .2 three .3 > three
15, Trochanter IV; number of setae (T)	one	.1 two .2 three .3 > three
17, Idiosoma; compression (T)	dorsoventral	lateral

18, Sejugal furrow; form (T)	clear furrow	.1 absent .2 indistinct band of striae
19, Adoral setae; number (T)	four	two
20, Adoral setae; form (T)	minute	long
21, Subcapitular setae; form (T)	of similar form	(<i>sbc₁</i>) reduced
22, Supracoxal setae (T)	absent	present
23, Palp tibiotalus; number of setae (T)	nine	.1 10 .2 > 10
25, Palp tibiotalus; form of I' (T)	normal	spiralled
26, Palp tibiotalus; form of solenidion (T)	erect	recumbent
27, Palp tibiotalus; form (T)	length > 3 times breadth	.1 length < 3 breadth .2 length = breadth
28, Palp genu; length (T)	> twice breadth breadth	.1 < twice breadth .2 = breadth
29, <i>cha</i> ; position (F)	proximal to fixed digit	on fixed digit
30, <i>chb</i> ; insertion type (F)	surface	pit
31, Epirostrum (T)	absent	present
32, Raised prodorsal eyes (T)	absent	present
33, Prodorsal shield (T)	absent	present
34, Dorsal idiosomal markings (T)	absent	.1 transverse .2 V- or Y-shaped .3 longitudinal
35, Prodorsal setae; number (T)	eight	.1 six .2 ten .3 > ten
36, (<i>iv</i>); position (F)	on naso	.1 at base of naso .2 behind naso
37, (<i>iv</i>); form (F)	filiform	expanded

38, (<i>f</i>); form (F)	filiform	expanded
39, Opisthosomal setae; number (F)	16	.1 10 .2 14 .3 > 17
40, (<i>c</i>) row; arrangement (T)	level	(<i>c</i> ₂) anterior to (<i>c</i> ₁)
41, (<i>f</i> ₁); form of base (T)	normal	bothridial
42, (<i>f</i> ₁); form (T)	normal	trichobothridial
42a, (<i>f</i> ₂); position (T)	<i>ca</i> , in line with (<i>f</i> ₁)	<i>ca</i> , posterior to (<i>f</i> ₁)
43, Lyrifissures; form (T)	round	slit-like
44, Coxal delimitation; extent (T)	widely separate proximally	.1 only distal margins clear .2 <i>ca</i> , contiguous proximally
45, Coxa II and III; arrangement (T)	separated	contiguous
46, Coxa I; form seta (<i>f</i> _c) (T)	same form as (<i>f</i> _b)	distinctly finer than (<i>f</i> _b)
47, Coxa III; number of setae (T)	four	.1 three .2 five .3 six .4 seven .5 > seven
48, Coxa IV; number of setae (T)	three	.1 two .2 four .3 > four
49, Delimitation outer margins genital shields (T)	indistinct	distinct
50, Genital setae; arrangement (T)	single file	.1 (<i>g</i> ₄) lateral .2 (<i>g</i> ₅) lateral .3 not as above
51, Genital setae; number (T)	12 or less	.1 14 .2 > 14
51a, Eugenital setae; form in o (F)	homeomorphous	heteromorphous
52, Aggenital setae; number (T)	10 or less	.1 14 .2 > 14
53, Anus; position (T)	subterminal	.1 terminal .2 dorsal

54. Anus; form (T)	slit-like	circular
55. Pseudanal setae; number (F)	six	four
56. Adanal setae (F)	absent	present
58. Femur IV; form (T)	slender	enlarged
58a, Leg I; form (T)	normal	antenniform
59. Apotele I; form (T)	normal	.1 reduced .2 elaborate
60. Famulus tarsus I; form (F)	normal	.1 elongated stalk .2 greatly enlarged
61. Famulus; tibia I (T)	present	absent
62. Rhagidial organs; form (F)	recumbent	semi-erect
63. Recumbent rhagidial organs; form (F)	L-shaped	.1 T-shaped .2 not as above
64. Tarsus II; form terminal setae (T)	simple	capitate
66. Famulus tarsus II; form (F)	normal	elaborately branched
67. Tarsus I; number of solenidia (F)	three	.1 two .2 four .3 > four
67a, Leg tarsi; erect solenidia (F)	absent	present
68. Tibia I; distal rhagidial organ (F)	present	absent
69. Tibia I; proximal erect solenidion (F)	absent	present
69a, Tibia I; number of rhagidial organs (F)	one	two
70. Genu I; rhagidial organ (F)	absent	present
71. Genu I; number of solenidia (T)	none	.1 one .2 > one
72. Tarsus II; number of solenidia (F)	three	.1 two .2 four .3 > four
73. Tibia II; number of rhagidial organs (F)	one	one
74. Tibia II; number of erect solenidia (F)	none	.1 one .2 > one

75, Tibia II; form distal rhagidial organ (F)	exposed	subcuticular
76, Flabellum (F)	absent	present
77, Genu II; rhagidial organ (F)	absent	present
78, Genu II; number of erect solenidia (F)	absent	.1 one .2 > one
80, Tibia III; rhagidial organ (F)	absent	present
80a, Tibia III; number of erect solenidia (T)	absent	.1 one .2 two .3 > two
81, Genu III; rhagidial organs (F)	absent	present
82, Genu III; number of erect solenidia (T)	absent	.1 one .2 > one
83, Tibia IV; rhagidial organs (F)	absent	present
84, Tibia IV; number of erect solenidia (F)	none	.1 one .2 > one
85, Genu IV; solenidia (T)	absent	present
87, Genua; distal papilla (T)	absent	present

Cladogram construction

The cladograms were constructed by hand. Although cladistic computer programs exist, those available could not economically or practically be used to compute a data matrix of the size compiled for this study. Besides which, as the study group was poorly known and an analysis of this kind had never previously been attempted, it was considered more advantageous to be able to re-examine specimens for further apomorphies should resolution of areas of the cladogram prove difficult.

The weighting system of Hecht & Edwards (1977) was not applied to the characters used in this study although less weight was given to the absence of a character.

Each of the four holophyletic groups were analysed separately by searching for nesting sets of apomorphies. Where overlap of sets occurred, those possessing the greatest numbers of congruent synapomorphies were recognised. Where part of a cladogram could not be explained by dichotomies but the taxa involved formed holophyletic groupings, polychotomies were included.

8.3.2 Results of the analysis

The cladograms in Figures 42-46 are hypotheses of holophyletic groupings representing supra-specific taxa within the superfamily Eupodoidea. The presence of a rather large number of parallelisms (denoted by a single prime ') is evident in several of the cladograms, an occurrence noted in other acarine taxa (André 1979). As these parallelisms are not, however, themselves congruent, they are not considered to indicate that the cladograms are not the most parsimonious.

The establishment of the superfamily as a holophyletic group, noted earlier, was based on the autapomorphies of the stellate form of the famulus of tarsus I (6a) and the presence of a famulus on tarsus II (7), a naso (8), three setae on the palp genu (9), recessed solenidia (rhagidial organs) on, at least, tarsus I (11) and a prodorsal shield (33).

It may be argued that in a small number of tydeoids, the solenidion of the palp tibiotarsus or of tarsus I is recumbent, resembling a rhagidial organ. In the Tydeoidea, however, there is no clear pit associated with the solenidion and so it is not regarded as homologous with a rhagidial organ. Conversely, in certain eupodoid taxa, the rhagidial solenidia are more or less erect but are always located in a smooth pit and so are regarded as homologues.

Holophyletic groups representing families (Fig. 42)

The cladogram demonstrates the formation of four holophyletic groups which, apart from in two aspects, conform to most traditional concepts of familial membership. The exceptions are firstly that the members of the Penthaleidae, sometimes included in the Eupodidae (Strandtmann 1971) or the Penthalodidae (Baker 1946, Cunliffe 1955), are identified as a discrete holophyletic group, justifiably independent. Secondly, the monotypic family Strandtmanniidae described by Zacharda (1979) is a redundant taxon and so is not recognised. A fuller discussion of this action is given in the following section. Applying the convention that traditional rankings of natural taxa should be retained, the four holophyletic groups are each given the status of family.

At the first dichotomy of the Eupodoidea, the family Rhagidiidae forms one branch, defined by the following autapomorphies:

- strongly hooked fixed digit (12.2);
- two cheliceral setae (13.2);
- two setae on trochanter III (14.1);
- long adoral setae (20);
- more than nine palp tibiotalarsal setae (23);
- a virtually round palp genu (28.2);
- coxae almost contiguous proximally (44.2);
- a terminal anus (53.1);
- the presence of adanal setae (56);
- the absence of a famulus on tibia I (61');)
- the subcuticular rhagidial organ of tibia II (75).

The second branch of the first dichotomy is defined by two character states, the spiralled ornamentation of palp tibiotalarsal seta 1' (25) and the presence of a recumbent palp tibiotalarsal solenidion (26).

Subsequently, the families Penthaleidae and Penthalodidae form a holophyletic group defined by the autapomorphies of the genital setae not arranged in single file (50) and a distal papilla on the leg genua (87).

Members of the Penthaleidae are defined by seven synapomorphies, four of which (14.2,.3, 15.2,.3, 39.3, 52.2) concern the more or less neutrichous chaetome of these mites. The other three are the robust nature of the palp tibiotalarsus (27.2) and genu (28.1) and the dorsal or terminal position of the anus (53).

Autapomorphies of the family Penthalodidae are:

- the absence of supracoxal setae (22);
- the presence of an epirostrum (31);

raised prodorsal eyes (32);
longitudinal or V-Y shaped idiodorsal markings (34.2,.3);
slit-like lyrifissures (43);
the limited and heavy delimitation of the leg coxae (44.1);
the distinct delimitation of the genital shields (49);
the absence of the famulus of tibia I (61').

The remaining group identified by the cladogram are those taxa conventionally classified in the family Eupodidae. This family, hitherto characterized by a combination of primitive characters, does not possess such immediately observable autapomorphies as were identified for the other families. A search for unique characters, however, discerned the presence of two rhagidial organs on tarsus I (67.1) and the reduced form of the basal subcapitular setae (*sbc*₁) (21) and coxal seta *1c* (46). It could be argued that the species *Eupodes ereynetoides* is ineligible for inclusion in a group with this definition since it apparently possesses only one rhagidial organ on tarsus I. Examination of the organ, however, reveals that there are two attachment points and it is, here, regarded to represent two rhagidial organs fused.

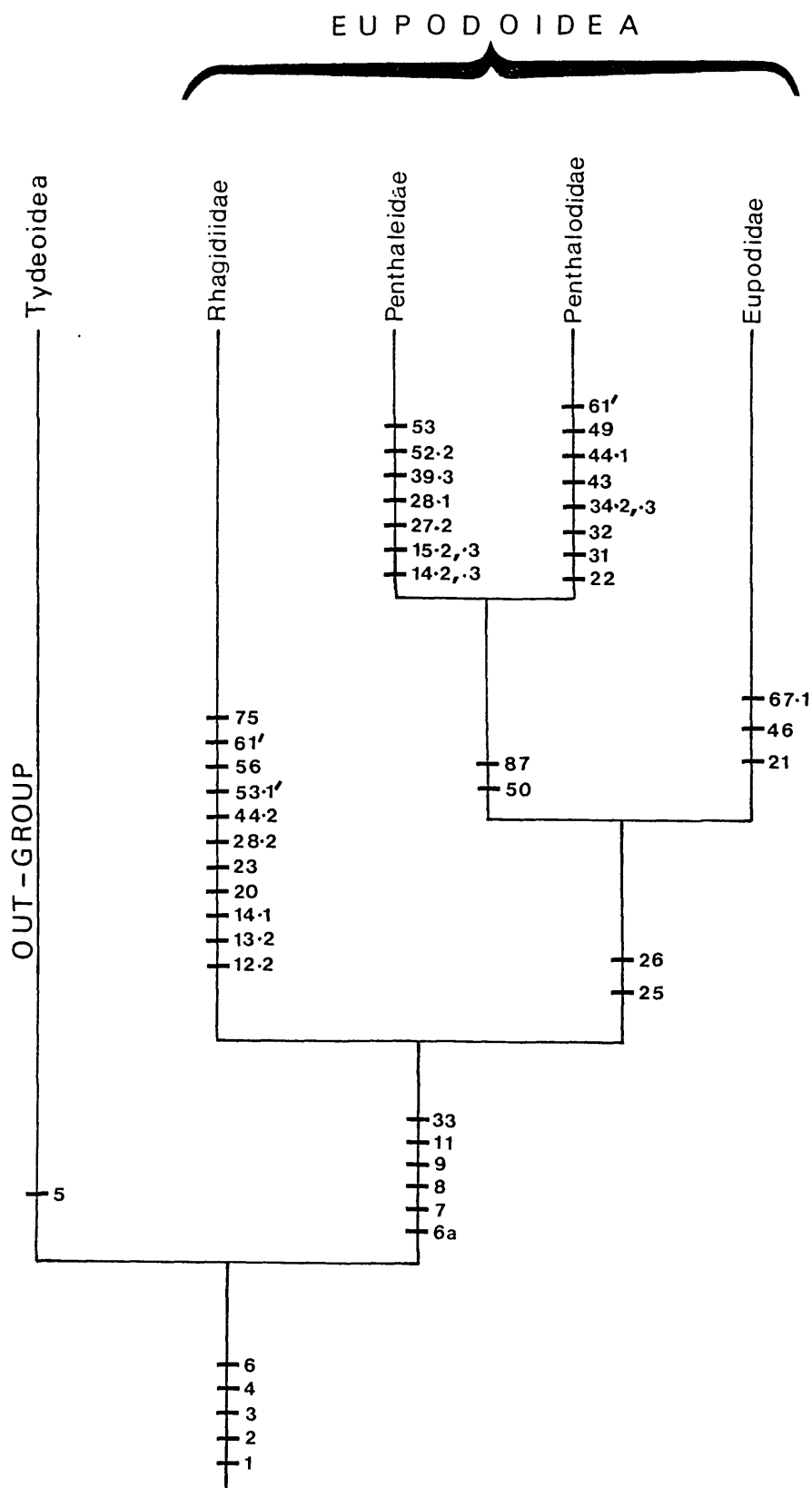


Fig. 42. Cladogram showing the initial division of the superfamily Eupodoidea into families. ' = a parallelism.

Holophyletic groups indicating genera

Rhagidiidae (Fig. 43)

The initial division of the family is treated as an unresolved polychotomy. The first clade resulting from this comprises those taxa with expanded prodorsal trichobothria (38) and is further subdivided into three holophyletic groups. The taxa *Pilorhagidia hirsuta* and *Strandtmannia celtarum* form one of these with the following autapomorphies:

three setae on trochanter IV (15.2);

five pairs of prodorsal setae (35.2);

neotrichous opisthodorsal chaetome (39.4);

respectively five and four setae on coxae III (47.2') and IV (48.2').

The presence of nine setae on the palp tibia-tarsus (23*) is regarded to be a reversal to the primitive condition. The two taxa in this group are congeneric, with *Pilorhagidia* Strandtmann & Goff 1978 taking priority over *Strandtmannia* Zacharda 1979. Zacharda (1979) also erected the new family, Strandtmanniidae, to accommodate *Strandtmannia* on the basis of the neotrichous chaetome and the presence of three pairs of pseudanal setae. Examination of the type material, however, established that a pair of adanal setae does, in fact, occur. To avoid maintaining a redundant taxon, the family Strandtmanniidae is not recognised. The existence of two species exhibiting the autapomorphies described were considered grounds for retaining the genus *Pilorhagidia*.

Hammenia macrostella possesses several unusual features, namely, one pair of adoral setae (19) and an enlarged, elaborately branched famulus I (60.2) and famulus II (66). It is also unusual amongst the Rhagidiidae in possessing only one cheliceral seta, a character which can be regarded as

a reversal to the primitive condition (13*), while the distal rhagidial organ of tarsus I is unique in being an inverted U-shaped (63.2).

Unfortunately, *H. macrostella* is the only taxon to exhibit these characters and, while the discovery of further species may support its establishment as a genus, this action cannot be justified at present.

The remaining taxa in this first clade differ from each other in the setal complement of the palp femur (10) and tibiotalrus (23), chelicera (13*) and coxa III (47) and in the solenidiotaxy of tarsi I and II (67, 72). This assemblage comprises the species *Parallelorhagidia evansi*, *Coccorhagidia clavifrons*, *Tuberosstoma gressitti*, *Arctorhagidia sateri*, *Eskimaia capitata* and *Brevipalpia minima*, the latter two being the representatives of monotypic genera. Despite reference to the species omitted from this study which Zacharda classifies in the remaining three genera, no justification could be found for retaining these taxa. Consequently, all of the above species along with *H. macrostella*, are classified in the genus *Coccorhagidia*. This is a rather unsatisfactory grouping in cladistic terms as it can only be defined by the homoplasious autapomorphy of expanded trichobothria and by primitive characters, i.e. by the holotrichous chaetome. On present knowledge, however, this is regarded to be the best solution in terms of utility.

Amongst the remaining taxa, i.e. those with filiform trichobothria, three holophyletic groups are identified which are given generic status. These are the species of *Latoempodia*, *Shibaia* and *Troglocheles*. In all cases, they possess apomorphies found to be shared by more than one species.

Latoempodia and *Shibaia* form a holophyletic group defined by the autapomorphies of cheliceral seta, *cha*, being located on the fixed

digit (29) and by the presence of, respectively, nine and five setae on the palp tibiotalus (23.1') and on coxa III (47.2'). These two taxa can then be separated on the basis of the multiple rhagidial organs present in *Shibaia* (67.2, 70, 72.1', 73, 77, 81, 83, 85) and the elaborate apotela I (59.2) of *Latoempodia*. The third holophyletic group, the genus *Troglocheles*, is unique amongst eupodoids in possessing capitate setae on tarsi II-IV (64) and multiple rhagidial organs on tarsus I (67).

The remaining species, defined by the presence of 10 or more palp tibiotalal setae (23), can be divided into holophyletic groups most parsimoniously on the basis of the setal complement of coxa III (47) and the tarsal solenidiotaxy (67, 72). In addition, other unique character states occur within these groupings but are apparently specific autapomorphies. None of the resulting associations are here regarded to represent genera and so all of these species are classified in the genus *Rhagidia*. This is an unsatisfactory situation since *Rhagidia* remains a large and heterogeneous group and it is felt that the problem warrants a further analysis including all known taxa and with a revised character set. Since such a task is beyond the scope of the present study, it is felt that the generic groupings proposed above represent the best scheme to permit identification of specimens and in which new data can be accommodated.

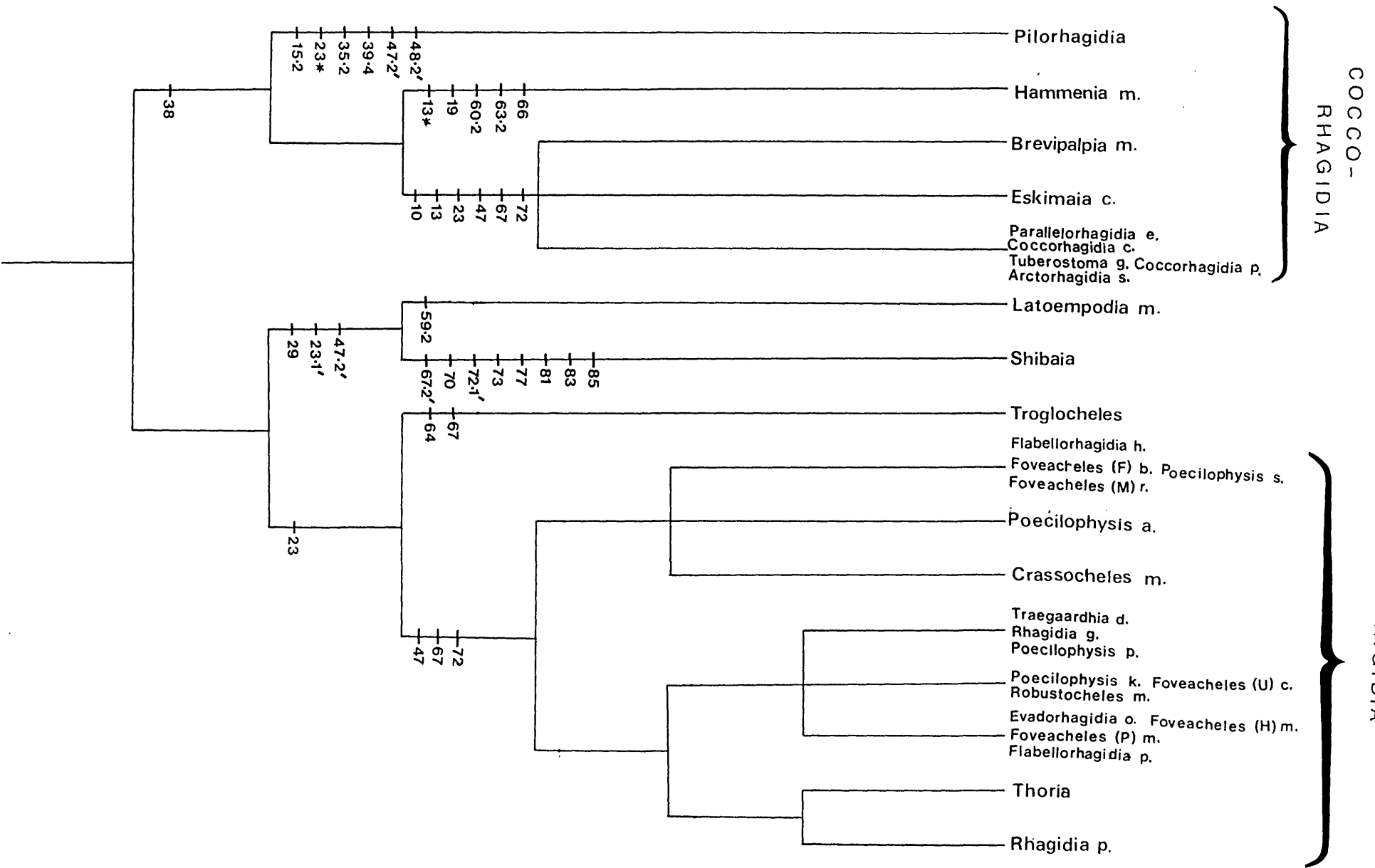


Fig. 43. Cladogram of the family Rhagididae.
' = a parallelism, * = a reversal.

Penthaleidae (Fig. 44)

Species of the family Penthaleidae form three holophyletic groups which are accorded generic status.

The genera *Linopenthaloides* and *Penthaleus* form a holophyletic group defined by autapomorphies concerning the strongly neutrichous chaetome (10.2, 14.3, 15.3, 35.3, 47.4,5, 48.2,3), the presence of erect solenidia on the leg tarsi (67a) and multiple solenidia on most of the leg segments (71, 74.2, 78.2, 80a.3, 82.2, 84.2, 85, 86). The subsequent dichotomy separates *Linopenthaloides novazealandicus*, defined by the contiguous coxae II and III (45) and the terminal position of the anus (53.1'), from the species of *Penthaleus* with the synapomorphies of a fixed digit terminating in a three-pronged terminal process (12a.1) and the dorsal position (53.2) and circular form of the anus (54).

The second branch of the initial dichotomy is occupied by the genus *Halotydeus* with the autapomorphies of trochantera III (14.2) and IV (15.1) being less strongly neutrichous, respectively three and two setae on coxae III (47.1) and IV (48.1) and the terminal position of the anus (53.1').

The redundant taxon *Linopenthaloides* is retained since the groupings resulting from its inclusion with either of the other two genera could not be unsatisfactorily defined.

Penthalodidae (Fig. 45)

The holophyletic groups identified agree with the conventional classification of the family into two genera. The genus *Penthalodes* can be recognised by the absence of cheliceral setae (13.1), the lack of external evidence of the sejugal furrow (18.1), the Y- to V-shaped furrow on the dorsum of the idiosoma (34.2), the hypotrichous opisthodorsal chaetome (39.1) and the presence of semi-erect rhagidial organs on tarsi I and II (62).

Stereotydeus, by contrast, possesses a sejugal furrow represented by striae (18.2) while the dorsal idiosomal markings are longitudinal (34.3).

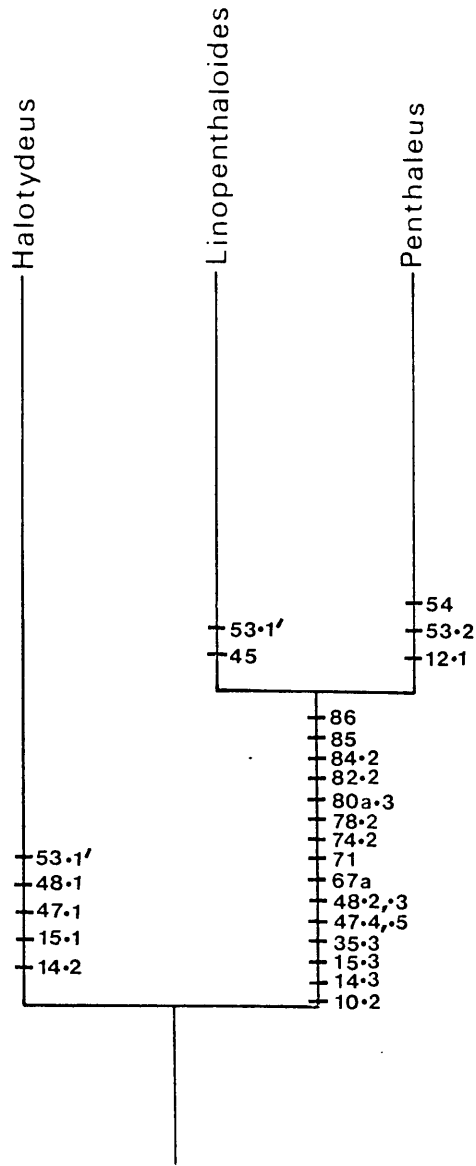


Fig. 44. Cladogram of the family Penthaleidae.
 ' = a parallelism.

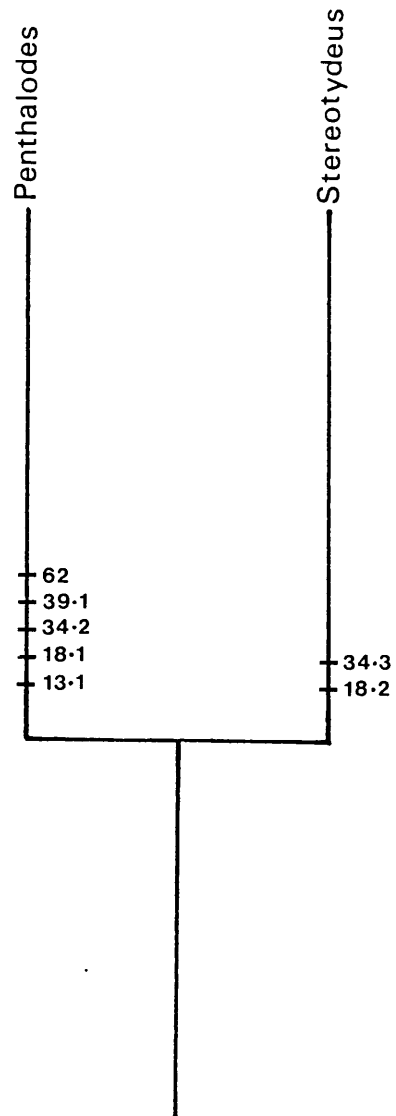


Fig. 45. Cladogram of the family Penthalodidae.

Eupodidae (Fig. 46)

The first dichotomy separates the taxa on the basis of the solenidiotaxy of tibiae I and II; in the taxa of clade 1, the proximal solenidion of these segments is rhagidiform (69a, 73) whereas, in those of clade 2, it is erect (69, 74).

At the first division of clade 1, one branch is defined by the autapomorphy of the presence of two pairs of pseudanal setae (55'). The first of the subsequent branches accommodates the species *Caleupodes reticulatus* and is defined by the autapomorphous presence of transverse furrows of the opisthodorsum (34.1), which are regarded to indicate primary segmentation, seven pairs of genital setae (51.1) and two rhagidial organs on tarsus II (72.1'). In addition, this taxon lacks a prodorsal shield (33*), a reversal to the plesiomorphic state. The new genus, *Caleupodes*, has been erected for this taxon (Baker, in press), and its retention can be criticized for creating a redundant taxon. The decision was based on the uniqueness of *C. reticulatus* and the inability to produce a satisfactory cladogram which delimits a holophyletic group of taxa to accommodate it. The second branch delimits those taxa with the sejugal furrow only present as a narrow band of transverse striae (18.2), opisthosomal seta (c_2) located anteriorly to c_1 (40), three setae on coxa III (47.1') and T-shaped rhagidial organs (63.1'). The taxa are further divided into two holophyletic groups; one is defined by the reduced chela (12a), the lateral position of genital seta g_4 (50.1'), the very long antenniform leg I (58a) and the reduced form of apotele I (59.1'), the second by the ovoid palp tibiotarsus (27.1'), internal vertical setae being located behind the naso (36.2) and the enlarged femur IV (58'). These two holophyletic groups respectively comprise the

species traditionally classified in the genera *Linopodes* and *Cocceupodes* and are both maintained with the status of genus. Certain members of *Cocceupodes* possess the apomorphies of expanded internal vertical setae (37) and the presence of a rhagidial organ on tibiae III (80') and IV (83). However, since the numbers of species involved are small and *Cocceupodes* is adequately delimited as a holophyletic group, it was decided not to further subdivide the genus.

The second branch of clade 1 is defined by the ovoid palp tibiotarsus (27.1') and the usual presence of a solenidion on tibia III (80', 80a.1). Six synapomorphies identified in the three species of *Claveupodes* establish them as a holophyletic group accorded generic status. The synapomorphies are as follows:

- internal vertical setae located at the base of the naso (36.1);
- expanded prodorsal trichobothria (38);
- idiosomal setae (f_2) located almost posterior to (f_1) (42a);
- anus terminal (53.1);
- two rhagidial organs on tarsus II (72.1');
- T-shaped rhagidial organs (63.1').

A second holophyletic group, comprising those taxa with solenidia on genua I to III (71.1', 78.1', 81.1), is further subdivided according to whether two rhagidial organs are present on tarsus II (72.1') or the rhagidial organs are T-shaped (63.1'). These two branches are both represented by one species, respectively, *Eupodes* 11 and *Eupodes* 9, but since taxa not included in this study fit one or other of the definitions (see Section 10 for more details), they are both accorded generic status.

Clade 2 first divides into a holophyletic group defined by the bothridial form of the base of opisthodorsal seta f_1 (41'), only two setae on coxa IV (48.1), two pairs of pseudanal setae (55') and an erect

solenidion on genu I (71.1') and II (78.1'). The group comprises *Eupodes* 8 & 13 and is accorded generic status. The second branch comprises those taxa with two rhagidial organs on tarsus II (72.1') and, subsequently, the species *Hawaiieupodes thermophilous* is isolated due to the lateral compression of the idiosoma (17), an ovoid palp tibiotarsus (27.1'), three setae on coxa III (47.1') and the absence of the famulus on tarsus II (61'). Despite being a monotypic and, therefore, a redundant taxon, the genus *Hawaiieupodes* is retained since no other satisfactory solution could be found. The position of this taxon is, however, somewhat tentative as characters were difficult to discern in the slide mounted type material, while certain details required were not given in its description.

The remaining species, defined by the synapomorphies of enlarged femora IV (58'), fall into two holophyletic groups. One comprises the three species with the synapomorphies of the presence of opisthosomal trichobothria in the *f*₁ position (42) and the lack of the famulus on tibia II (61'). These three species include *Benoinyssus najae* Fain, the type species of the genus. Since the only diagnostic character that Fain (1958) describes is the presence of opisthosomal trichobothria, this group is accorded generic status with the name of *Benoinyssus*. One of the three members, *Eupodes ereynetoides*, is unique due to the bridge-like tarsal rhagidial organs (63.2). Again, the two attachment points of the rhagidial organ are taken to indicate the fusion of two organs. In addition, *E. ereynetoides* differs from the other two species because the fourth pair of genital setae is located laterally to the others (50.1'). Although this may suggest a basis for further subdivision of these taxa, the number of species involved is too small to sensibly justify this, especially when they can be satisfactorily defined by the autapomorphy of the presence of opisthosomal trichobothria.

The second holophyletic group comprises those species with genital seta (g_4) located laterally to the other genital setae (50.1') and the heteromorphous eugenital setae of the female (51a). The member taxa are those traditionally classified in the genus *Eupodes* plus *Egypteupodes strandtmanni*. *E. strandtmanni* is unique amongst eupodoids in lacking internal vertical setae (35.1) and it is this character that was originally used to diagnose the genus. Since *E. strandtmanni* matches the *Eupodes* species in all other respects and, furthermore, can only be defined by a loss character, *Egypteupodes* is not given generic status. Similarly, *E. angardi* is unusual amongst these species in possessing a rather slender femur IV (58*), but agrees in all other aspects. This feature is considered to represent a reversal to the plesiomorphic condition and its possession does not exclude *E. angardi* from the group. It is worth noting here that the remaining species of *Eupodes* all lack a distal rhagidial organ on tibia I, only the famulus being present (68), and seven pairs of aggenital setae (52.1). In certain other species, however, including *E. strandtmanni* and *E. angardi*, a distal rhagidial organ is present and there are five pairs of aggenital setae.

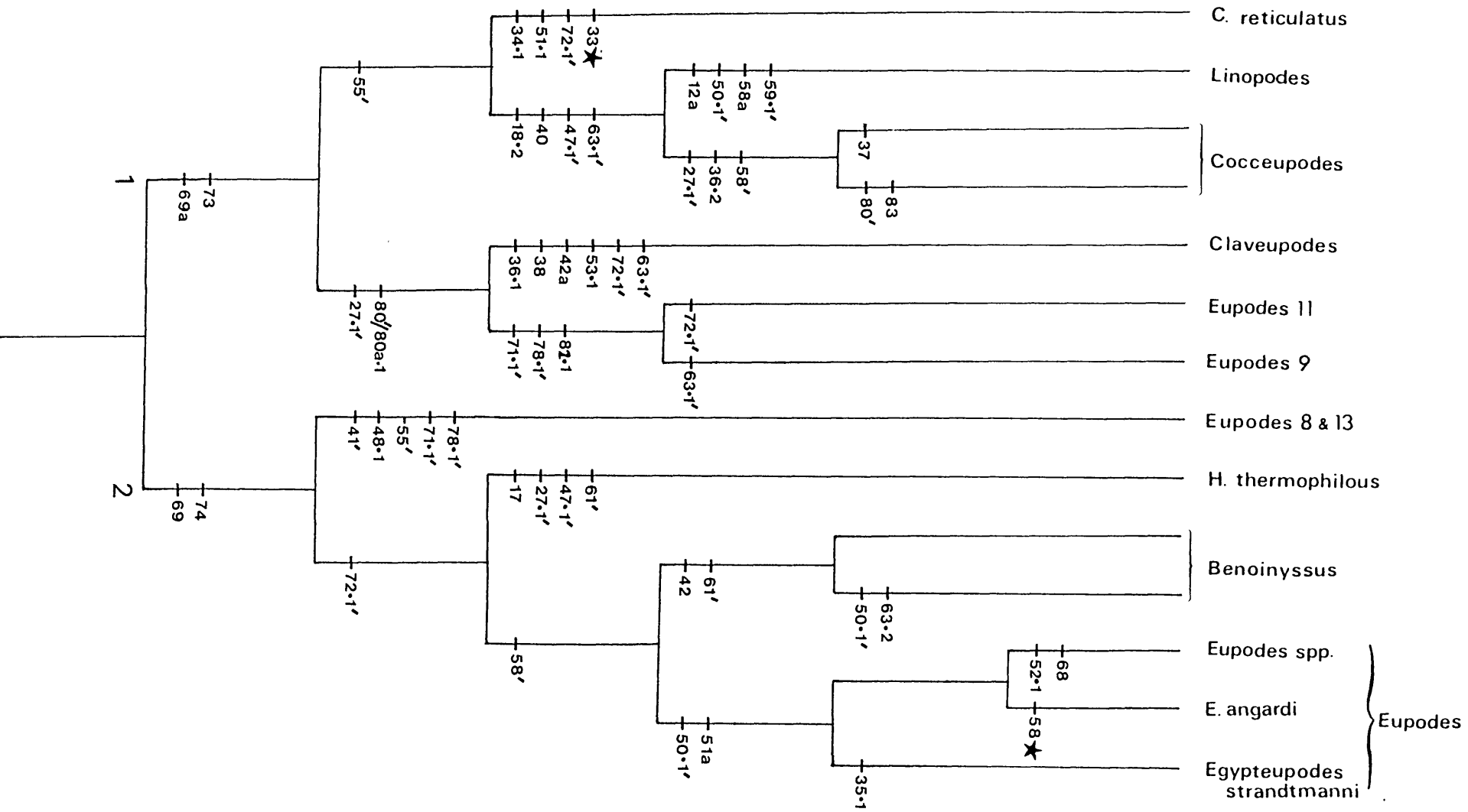


Fig. 46. Cladogram of the family Eupodidae.
 ' = a parallelism, ★ = a reversal.

8.3.3 Survey (see section 8.4 for a full discussion)

The analysis successfully divided the superfamily into four families, three of which (the Penthaleidae, Penthalodidae and Eupodidae) could be further subdivided into genera. In the family Rhagidiidae, however, the taxa were divided into a number of holophyletic groups, some of which are accorded generic status but the majority are not regarded to comprise taxa that satisfactorily indicate valid genera. A number of species possessed autapomorphic characters which may prove to define genera but, since they are monotypic and so redundant taxon, they were not accorded generic status.

The classification proposed for the Rhagidiidae is considered to be far from satisfactory and it was concluded a further study is needed encompassing all known taxa and with a reconsidered character suite. Since this was considered to be beyond the scope of the present study, a utilitarian solution was proposed which would facilitate the easiest identification of species and permit the accommodation of additional data.

The cladistic analysis was found to be more successful than the phenetic; a conclusion also arrived at by Niedbala (1986) in his study of the Phthiracaroida. Whether it would have pleased disciples of cladistics though is open to question due to the incorporation of the utilitarian aspect. This has resulted in taxa in the proposed supra-specific classification which could not be described by apomorphies, but which could not be placed elsewhere, being maintained and diagnosed in terms of plesiomorphies and loss characters.

8.4 A DISCUSSION OF SYSTEMATIC METHODS AND THEIR APPLICATION TO THE EUPODOIDEA

Before the implications of the phenetic and cladistic analysis upon eupodoid classification is considered, it is necessary to discuss the essential differences between the principal schools of systematics, viz. phenetics, cladistics, evolutionary biology and traditional. Detailed discussions of the relative merits of the different methods can be read in the many papers that have been published by protagonists (for example, Mayr, 1965, 1969, 1974, Sokal & Camin 1965, Sneath & Sokal 1973, Rosen 1974, Hennig 1975, McNeill 1979, Farris 1977, 1979, Eldredge & Cracraft 1980, Patterson 1980, Charig 1981, Wiley 1981, Cracraft 1983, Funk 1983, Abbott *et al* 1985). Here, however, I shall just consider the major points at issue.

Agreement between the various schools apparently does not extend past the recognition of the *need* to arrange organisms into a system (=classification) which comprises natural groups, conveys maximal information and enables the most forecasts to be made about characters and taxa not included in the classification. The disagreement concerns the identity of the method which produces the classification to fulfil these functions. To summarize:

- a) cladistic analysis is criticized for being primarily interested in resolving genealogy at the expense of maximising character information and, hence, predictive value of the classification, for ignoring 'facts' of evolutionary process and for subjectively weighting characters;
- b) phenetic methods are criticized for not considering phylogenetic information, for giving all characters equal weighting and for

grouping on overall similarity;

c) evolutionary biologists are criticized for not having a clearly stated methodology, for subjectively weighting characters and for trying to accommodate the rate of evolutionary change in their classifications;

d) traditional taxonomists are accused of using systematics purely as a cataloging system for organisms.

Pheneticists apparently attempt to defuse the conflict between the different schools by their contention that the respective products need not be mutually exclusive but, rather, fulfil different functions. Hence, the phenetic method should be used to construct classifications, while cladistics produces evolutionary trees. The pheneticists view that any inclusion of phylogenetic information is undesirable in a classification is justified on the basis that it is impossible to *know* phylogeny. Cladists and evolutionary biologists, by contrast, see a classification lacking a phylogenetic element as unbalanced and generally useless, regarding groups that are not composed of descendants of a common ancestor as artificial and of low predictive value.

The phenetic principles of using unweighted characters and of grouping on raw overall similarity is based on the belief that, providing the number of characters considered is large enough, the genotype will be accurately represented. Proponents of the other schools, however, criticize this reasoning as they regard the relationship between genotype and phenotype to be much more complex. As Mayr (1969) states:

'The visible phenotype is as small a fraction of the total potential phenotype as the visible part of an iceberg is of the whole'.

In their consideration of characters, pheneticists discount the risk that similarity due to convergent or parallel evolution will cause a

misleading picture of overall similarity. It is assumed that, in higher taxa, such instances would occur only in a minority of characters and so would not unbalance the analysis, while, at the generic or specific level, homoplasies are regarded to be undetectable. In any case, pheneticists conclude that the detailed analysis and coding of characters advocated for their method will highlight the subtle differences in similarity in organs due to convergent or parallel evolution and, therefore, their inclusion will not affect the classification. *A priori* weighting of characters is regarded as subjective.

Proponents regard groupings produced by phenetic methods to be the most natural of all the methods. 'Natural' is used in the sense of Gilmour (1940, 1961), whereby the more natural a classification, the more conclusions can be drawn about its constituent groups. This is translated by pheneticists to mean that members of a natural group will have many characters in common and, hence, equates with their concept of grouping according to overall similarity.

Pheneticists prefer polythetic groupings (those in which most of the members of a group possess most of a given set of characters) in their classifications. By not using a restricted definition or insisting on complete character correspondence of taxa, pheneticists believe that subsequently discovered organisms which lack just one of the defining characters are less likely to be misclassified. In addition, polythetic groups are regarded to allow greater predictability.

Finally, pheneticists claim that their method is the most objective, as it only requires that characters be observed and recorded, and that it is suitable for any group of taxa because of this.

As outlined in Section 8.3, cladists are concerned with the establishment of and relationship between holophyletic groups defined by

evolutionary novelties, *i.e.* by synapomorphies. Evolution is considered to be achieved by the splitting of taxa (cladogenesis) and so the influence of selection pressures is not reflected. Holophyletic groups cannot be defined by primitive characters, *i.e.* by plesiomorphies, or, according to most cladists, by lack of characters as they are both regarded to be irrelevant.

Cladists disagree with the view outlined above that the different analyses should be used for different purposes since they consider their method, in addition to providing a genealogy, conveys more character information than does phenetics. The work of Mickevich (1978) is quoted by cladists as evidence that not only do cladistic methods produce natural classifications in the sense of Gilmour but that they also do so more successfully than the phenetic method. Mickevich computed various data sets using both phenetic and cladistic methods for each of a large number of groups of organisms. She found that the phenetic classifications differed much more widely than the cladistic.

Cladists reject the criticism levelled by opponents that they underestimate the difficulties of establishing character polarity but, instead, see this procedure as an objective method of weighting. Cladists do not claim, as opponents state, to definitively resolve phylogeny but rather to represent the best hypothesis of it. Indeed, the school of transformed cladistics, as described by Platnick (1979), believes that the evolutionary element is not essential and so may be omitted, the cladogram representing the simpler concept of the pattern of apomorphies in nature. In cladistics, the difference between similarity caused by homoplasy is stressed and it is necessary to identify such occurrences in an analysis.

As for information and predictability, cladists argue that no matter how a classification is produced, the information content for each member taxon in the hierarchy can only be its diagnosis and as this, in fact, only deals with the differences between them, the myriad shared primitive characters in the measurement of overall similarity provide no information. Furthermore, overall similarity will include characters which do not define natural groups. Cladists point out that the polythetic grouping favoured by pheneticists allows the members of a Gilmour-natural taxon and the distribution of a feature within it to not quite match. Consequently, this taxon cannot very well be said to describe the distribution of the feature, or *vice versa*, and so character information and predictive value is not, in fact, maximised. This implies that the set of correlated features upon which a natural taxon is based must not only be shared by its members but must also be largely restricted to that taxon. Hence, a natural taxon could be natural only if there was some set of well-correlated features which distinguishes just that one from all other taxa. Essentially, therefore, cladists regard a system of nesting synapomorphies to be more suitable for producing a hierarchy of natural taxa than is a general suite of similarities.

Cladists dispute the claim that a phenetic analysis can be carried out on any group, pointing out that it is the theoretical framework on which the classification is produced that is subjective and not the observations of the organisms.

Evolutionary biologists (also sometimes called syntheticists, while Funk (1983) refers to them as traditionalists) do not normally detail their methodology, there being no hard and fast rules. The procedure seems to vary but elements of both phenetics and cladistics can be identified. Mayr (1974) outlines his approach as follows. The taxa are

usually separated into groups based on a small number of 'important' characters and, within these, the taxa are arranged by observable overall similarity. The 'importance' of a character is measured by the intuition of the worker, while the assessment of overall similarity is apparently based on a visual impression. Evolutionary biologists include the aspects of time and selection pressures in their concept of phylogenetic process and reflect this in their classifications. Groups are ranked according to their level of organization, those at a similar level, termed grades, are given equivalent rank. Grades are regarded as monophyletic by evolutionary biologists but can, according to cladistic definitions, be holo- and/or paraphyletic. They are identified as significant evolutionary groups using one or more of the following criteria:

1) Morphological gap.

If two sister taxa are sufficiently different morphologically, they can be separated and placed in equivalent groups. This gap is inversely proportional to the size of the group.

2) Group size.

A group comprising many species is given a higher rank than a sister group with only a few members.

3) Adaptive zones.

A group judged to occupy a unique adaptive zone may be given higher rank than its sister taxon which does not.

Evolutionary biologists consider that their method conveys the greatest amount of information by using both branching points and degrees of evolutionary divergence to delimit taxa. Opposing this, cladists argue that it is impossible to observe or measure the influence of adaptive zones and so the uniqueness of a taxon must define it. Cladistics and phenetics are seen by evolutionary biologists as opposite

extremes - cladists ignore the important information concerning relationship contributed by shared ancestral characters, while pheneticists regard all characters to be equally important but reject a phylogenetic component. Evolutionary biologists accuse cladists of ignoring numerous 'facts' of evolution and phylogeny and of redefining established terms, in particular, monophyly. Other attributed shortcomings of cladistics include the failure to take into account the existence of and size of discontinuities between taxa and the concept that the parental species splits into two daughter species. The cladists view that evolution proceeds in the most simplest, *i.e.* the most parsimonious, way is disputed by evolutionary biologists who give examples, such as the case of mammals returning to an aquatic environment to refute this view.

Having carried out a phenetic and cladistic analysis on certain species of the Eupodoidea, it is difficult to then objectively predict how a classification produced by an evolutionary/traditional approach might have differed. Recollection, however, of the impression of valid groupings that develops whilst examining specimens and reading the works of other authors helps to make an assessment. It is acknowledged that the process includes elements of both cladistics and phenetics in that unique characters are heavily weighted and used for initial grouping but that, if these are not evident or those that are unique are not judged important by the user, then relationships are judged on the basis of overall similarity. The pressure of adaptation to different niches is not considered to make a large contribution to eupodoid systematics, since, apart from rhagidiids, the members occupy a similar niche. In the case of the Rhagidiidae, their adaptations for a predatory life style, in

particular the strongly chelate chelicerae, are obvious and serve to separate them from the other eupodoids in all analyses.

Beginning with the divisions into families, the Strandtmanniidae would have been retained in an evolutionary analysis; the fact of it forming a redundant taxon being irrelevant since the strongly neutrichous chaetome would be accorded sufficient weight to justify its separation. An evolutionary approach would certainly have agreed with the cladistic analysis in that a division into the families Eupodidae, Penthlodidae, Penthaleidae and Rhagiidae would have been identified. This is due to diagnostic characters, such as the unique form of the palp and presence of an epirostrum, being highlighted from amongst the mass of other shared characters. The respective diagnoses of the families would, however, have differed due to characters regarded as irrelevant by cladists being admissible to group taxa. Since this difference in attitude to characters revolves around the acceptance (cladists) or rejection (evolutionary biologists) of dichotomous speciation (= cladogenesis) and whether or not primitive characters are retained irregularly, the two sides of this argument seem to be irreconcilable. The evolutionary biologist's viewpoint, however, results in more characters being available for grouping. This particularly affects the family Eupodidae which, as a consequence, could be diagnosed by a combination of primitive and loss characters, viz. the absence of an epirostrum, the subchelate chelicerae and slender palps. These would have been deemed more important than the diagnostic apomorphies of the presence of two rhagidial organs on tarsus I, reduced subcapitular and coxal setae identified in the cladistic analysis. It is likely, however, that a closer relationship would have been accorded to the families Eupodidae and Penthaleidae than to the Penthaleidae and Penthlodidae.

This is due to the shared possession by eupodids and penthaleids of plesiomorphous characters, such as the absence of an epirostrum and similarity of idiodorsal markings, being given greater weight than the presence of genual papillae, an apomorphic character uniting the Penthaleidae and Penthalodidae.

The generic groupings produced by the phenetic and cladistic analyses are not, on the whole, very different (see Table 8, p. 227). Areas of conflict concern the status of the taxa *Eupodes* 8, 9 and 11, *Caleupodes reticulatus* and *Hawaiieupodes thermophilous*. In the phenetic analyses, these species were isolated taxa but showed the greatest overall similarity to each other so that it would be possible to classify them in a single polythetic genus. In the cladogram of the family Eupodidae, character analysis provided more convincing evidence for the separation of these species on the basis of differences in the solenidiotaxy. Furthermore, it is felt that the inclusion in the phenetic analysis of *Eupodes* 13 (the British species found after analyses were complete) would have resulted in yet another monotypic 'genus' since the relatively large differences in dimensions would have masked the sharing of the unique complement of only two setae on coxa IV. In the cladistic analysis, this character state was identified as an autapomorphy and so caused the separation of the taxa possessing it. In addition, the cladistic analysis more clearly demonstrated the affinities of *Egypteupodes strandtmanni* and *Eupodes angardi*.

The genus *Egypteupodes* would have been retained in a traditional classification, the unique absence of the internal vertical setae would have been considered important enough to warrant separation. Apart from this, the remaining generic groupings would have matched those of the cladistic analysis. The relationships, however, would have been somewhat

different, measurement of affinities being based on overall similarity only in those characters judged to be relevant by the worker. In the family Penthaleidae, for example, the greater affinity would be recognised between the genera *Halotydeus* and *Linopenthaloides* since they share the same form and position of the anus. These two character states were not utilized in the cladistic analysis because they were identified as plesiomorphies. In the case of the Eupodidae, the genera *Cocceupodes* and *Linopodes* would have been accorded a close relationship as in cladistic analysis, but would have occupied a more isolated position because the other taxa would be grouped together on the primitive character of the presence of a clear sejugal furrow. The remaining taxa would then be grouped on the complement of tarsal rhagidial organs and pseudanal setae, the form of the palp tibiotarsus and femur IV and the arrangement of the genital setae. Hence, *Hawaiieupodes* would be accorded a greater affinity with *Eupodes* 11 while *Caleupodes* and *Claveupodes* would be more closely associated with *Eupodes* s.str. (i.e. *Eupodes* 1, 3, 6, *E. alaskanensis*). *Hawaiieupodes* would be considered to be more closely related to *Eupodes* 11 than to *Eupodes* s.str.. Of the taxa with a distinct sejugal furrow, *Eupodes* 8 and 9 would be regarded to show the closest relationship to the *Cocceupodes/Linopodes* group.

When applied to the Rhagidiidae, neither the phenetic nor cladistic method of analysis was wholly successful and it is concluded that a reconsideration of the classification of this family is required utilizing a revised set of characters and including all species. Based on the data of the present study, an evolutionary approach would certainly have recognised the genus *Coccorhagidia* due to the possession of expanded trichobothria, while the other genera delimited by cladistic analysis would also be retained. The primitive states of the trichobothria, tarsal

setae, arrangement of the tarsal rhagidial organs and position of famulus I would have been used to define *Rhagidia*.

The variable success of the phenetic analysis when applied to the Eupodoidea is here attributed to its inability to highlight the shared possession of unique characters when taxa differ in a large number of those regarded to be of less value. Furthermore, other works are also considered to demonstrate the cladist's claim that groupings produced by phenetic analyses are not necessarily natural because the characters which produce them are not invariably 'good' taxonomic characters. An example can be seen in the study of a collection of antarctic eupodids carried out by Booth *et al* (1985). The data set used was composed entirely of setal lengths and, by gradually reducing the data set by those characters that made least contribution, the individuals eventually formed two clusters, each designated as a 'subspecies'. The only distinguishing features by which these two taxa could be diagnosed were small differences in the lengths of opisthodorsal setae. Differences of a few microns between setal lengths are not considered 'good' taxonomic characters, not least because errors can so easily occur when making measurements at this level. Hence, a problem of phenetics, as interpreted here, is that if the data set devised is large there is the risk that valuable taxonomic characters are masked but that, if it is restricted, there is less chance that the genotype will be adequately reflected. Similarly, opponents of cladistics argue that, by ignoring ancestral (=plesiomorphic) character states, a cladistic analysis will produce anomalous groupings. Since the terms plesiomorphic and apomorphic, however, are relative, plesiomorphic character states at a particular level would have been apomorphic at a lower one and consequently all character states are considered at some stage.

A merit of both phenetic and cladistic methodology is that their use encourages a detailed examination of specimens and a careful search for and appraisal of characters, whereas a traditional/evolutionary approach, perhaps, relies too heavily on those characters which are immediately obvious to the worker or are conventionally utilized for the particular group under study. If, however, it is accepted that some characters are more useful than others for producing natural groupings, then some measure of weighting must be incorporated. Consequently, the cladistic method is here concluded to have been more successful in classifying the Eupodoidea than the phenetic since the procedure for character analysis highlighted those states which are considered more valid for defining natural groupings. It may be argued that the utilitarian decisions concerning the retention of certain redundant taxa and the generic groupings which could not be satisfactorily defined by autapomorphies owe something to a traditional approach and, therefore, the two classifications could be expected to resemble each other. However, these actions were only taken to preserve the predictive element of the classification until further analyses suggested a better solution. Since the majority of groupings in the cladograms conformed strictly to cladistic methodology, this utilitarian aspect does not devalue the classification arrived at.

Despite the favouring of cladistics over phenetics, it is felt that the difficulty of establishing character polarity should not be underestimated. In this study, it was possible to polarize the majority of the characters because a satisfactory out-group could be identified but, in many other acarine taxa, by contrast, the establishment of such a group is not possible. Niedbala (1986), for example, could not determine the sister-group of the superfamily Phthiracaroidea and so concluded that the

only alternative was to establish polarities on the basis of common equals primitive, a procedure not accepted by many cladists.

Both phenetic and cladistic methods are said by their supporters to be repeatable and applicable to all groups. From the arguments, however, the claim is apparently based on the situation where a particular data matrix is provided. If this same information was given to a traditional or evolutionary biologist, it is predicted that the results would differ depending on the 'intuition' of the user. Although there are generally accepted criteria by which to distinguish valuable taxonomic characters (reviewed in Goto (1982), see also Le Quesne (1969)), in taxonomic studies it is invariably the task of the worker to choose the characters and code their states (in phenetics) or determine their polarity (in cladistics). All of these procedures represent choices which are subject to variation attributable to the worker and depend on him/her making the 'right' decisions.

The establishment of a systematic method which produces consistent and objective results is most desirable. Of the available methods, it is here considered that cladistics approaches this role since the concepts of apomorphy and parsimony incorporate both a stated methodology and a means for testing the resulting classification that are lacking in the others. Although the revised supra-specific classification proposed for the Eupodoidea (see section 9) is based on the cladistic analysis, it was concluded that where, for whatever reason, the cladogram could not be satisfactorily resolved, it was necessary to contribute an intuitive judgement to maintain the predictive element of the classification.

Table 8. Comparison of supra-specific classifications resulting from phenetic and cladistic analyses.

→ indicates generic grouping to which taxon belongs in alternative classification.

	PHENETIC		CLADISTIC
Family	<u>Rhagidiidae</u>		<u>Rhagidiidae</u>
Genus	<i>Pilorhagidia</i>		<i>Pilorhagidia</i>
	<i>Hammenia</i>	→	<i>Coccorhagidia</i>
	<i>Shibaia</i>		<i>Shibaia</i>
	<i>Thoria</i>	→	<i>Troglocheles</i>
	<i>Brevipalpia</i>	→	<i>Rhagidia</i>
	<i>Rhagidia</i>	→	<i>Rhagidia</i>
	<u>Eupodidae/Penthaleidae/</u>		<u>Penthaleidae</u>
	<u>Penthalodidae</u>		
	<i>Eupodes</i>		<i>Halotydeus</i>
	<i>Benoinyssus</i>		<i>Linopenthaloides</i>
	<i>Cocceupodes</i>		<i>Penthaleus</i>
	<i>Linopodes</i>		<u>Penthalodidae</u>
	<i>Claveupodes</i>		<i>Penthalodes</i>
	<i>E. angardi</i>	→	<i>Stereotydeus</i>
	<i>Egypteupodes s.</i>	→	<u>Eupodidae</u>
	<i>Hawaiieupodes t.</i>		<i>Caleupodes r.</i>
	<i>Eupodes 8</i>		<i>Linopodes</i>
	<i>Eupodes 11</i>		<i>Cocceupodes</i>
	<i>Caleupodes r.</i>		<i>Eupodes 11</i>
	<i>Eupodes 9</i>		<i>Eupodes 9</i>
	<i>Halotydeus</i>		<i>Eupodes 8 & 9</i>
	<i>Stereotydeus</i>		<i>Hawaiieupodes t.</i>
	<i>Penthalodes</i>		<i>Benoinyssus</i>
	<i>Linopenthaloides</i>		<i>Eupodes</i>

9. A PROPOSED REVISION OF THE SUPRA-SPECIFIC CLASSIFICATION OF THE
SUPERFAMILY EUPODOIDEA

Based on the cladistic study, the supra-specific classification of the Eupodoidea is shown in Table 9.

Many of the characters traditionally used by taxonomists to describe eupodoids were utilized in the classification, but now the taxonomic level which they define has been identified. Similarly, the majority of the taxa traditionally recognized have been retained but with amended definitions (see section 10). Diagnostic characters can also be obtained from cladograms (Figs 42-46).

9.1 FAMILIAL CLASSIFICATION

The four families into which, according to this study, the superfamily is divided largely conform to modern concepts (as given, for example, in Krantz 1978) in that no genus has been transferred to a different family. The monotypic family Strandmanniidae, however, was not recognised, the genus *Pilorhagidia* (this takes priority over *Strandtmannia*) being included in the Rhagidiidae.

Although most modern workers now recognise the Penthaleidae as a distinct family, it has relatively recently been classified both in the family Penthalodidae (Baker 1946, Cunliffe 1955) and Eupodidae (Baker & Wharton 1952, Strandtmann 1971). The discreteness of the family is concluded to have been confirmed by this study.

Table 9. A revised supra-specific classification proposed for the superfamily Eupodoidea.

Superfamily Eupodoidea Banks 1894

Family Eupodidae C. L. Koch 1842

Genus *Eupodes* C. L. Koch 1835

Alloeupodes n.gen.

Aneboeupodes n.gen.

Benoinyssus Fain 1958

Caleupodes n.gen.

Claveupodes Strandtmann & Prasse 1976

Cocceupodes Thor 1934

Hawaiieupodes Strandtmann & Goff 1978

Linopodes C. L. Koch 1835

Subeupodes n.gen.

Family Penthaleidae Oudemans 1931

Genus *Penthaleus* C. L. Koch 1835

Halotydeus Berlese 1891

Linopenthaloides Strandtmann 1981

Family Penthaldidae Thor 1933

Genus *Penthalodes* Murray 1877

Stereotydeus Berlese 1901

Family Rhagidiidae Oudemans 1922

Genus *Rhagidia* Thorell 1871

Coccorhagidia Thor 1934

Latoempodia Zacharda 1980

Pilorhagidia Strandtmann & Goff 1978

Shibaia Zacharda 1980

Troglocheles Zacharda 1980

Fain's (1958) division of the family Eupodidae is not supported. When erecting the genus *Bencinyssus*, he established the subfamily Bencinyssinae to accommodate it. The definitive characters of both taxa were given as the presence of opisthosomal trichobothria, five free palpal segments and the absence of eyes. The remaining genera in the family, which were said to lack opisthosomal trichobothria and possess four palpal segments and eyes, were classified in the subfamily Eupodinae; thus creating a very unbalanced division. The presence or absence of eyes is not a reliable taxonomic character in the Eupodidae since they are not consistently seen even in examples of the same species, their appearance apparently depending on the extent of clearing of the preparation. Furthermore, examination of type material of *B. najae* revealed the presence of the normal complement of four free palpal segments. This subdivision of the Eupodidae has not gained recognition and the subfamily Bencinyssinae, here regarded as a redundant taxon, is not retained.

9.2 GENERIC CLASSIFICATION

Proposed changes in generic classification only concern the families Eupodidae and Rhagidiidae. In the other two families, the Penthaleidae and Penthalodidae, the generic membership is unchanged but definitions are amended.

In the Eupodidae, the most change occurs in the classification of the species of the genus *Eupodes*. The heterogeneous assemblage of species included at the commencement of this study could not be satisfactorily defined. Differences occurred in solenidiotaxy, form of the palp

tibiotarsus and setal complements of the coxae and pseudanal segment; certain of the species are now accommodated in other genera.

Of the characters given in Koch's cursory description of *Eupodes*, the only one recognizable today is the presence of a swollen femur IV. This, however, could apply to members of the genera *Cocceupodes* and *Benoinyssus*, as well as to the majority of species of *Eupodes*, and so cannot be regarded as a diagnostic character for *Eupodes*. Consequently, the classification here proposed does not exclude species with slender femora IV (such as *E. angardi*) from the genus if they conform with all other aspects of *Eupodes*.

Within *Eupodes*, two species groups can be discerned, those with a distal rhagidial organ on tibia I and five pairs of aggenital setae, for example, *E. angardi*, *E. strandtmanni*, and those lacking this distal organ and possessing seven pairs of aggenital setae, for example, all four species found in Britain. All other generic characters, however, are shared and, at present, the genus is retained intact.

The genus *Egypteupodes* is not retained since examination of the type material shows that the only difference between *E. strandtmanni*, its only member, and species of *Eupodes* is the absence of internal vertical setae. This is not considered sufficient to justify the retention of a monotypic genus and, consequently, *E. strandtmanni* is transferred to *Eupodes*.

The membership of the genus *Benoinyssus*, formerly a monotypic taxon, is increased to three by the transfer of *Eupodes ereynetoides* Strandtmann & Prasse and *Eupodes momeni* Abou-Awad. As described in the taxonomic analyses, there is some variation in genital setation and the form of the tarsal rhagidial organs. Subdivision, however, would be unproductive due to the small numbers involved. Should more species be discovered, the problem might be clarified.

Four new eupodid genera are erected. The members of two, *Alloeupodes* and *Subeupodes*, comprise species previously classified in the genera *Eupodes* or the now invalid *Prottereunetes* and are separated on the basis of the solenidiotaxy and form of the palp tibiotarsus.

Aneboeupodes is erected to accommodate those species with respectively four and two setae on coxal III and IV. Although, to date, only two member species have been described, it was considered valid to erect this genus since, in this study, coxal setation has been identified as constant within genera.

The fourth genus is monotypic, comprising the new species *C. reticulatus* (Baker, in press). This is unique amongst eupodoids in possessing evidence of external primary segmentation and amongst eupodids for possessing reticulate patterning. Although ornamentation of the integument is not regarded as an important taxonomic character, it does tend to be of a similar form within acarine genera. That apart, the unique combination of coxal and pseudanal setation and solenidiotaxy precludes it from membership of any of the other genera.

It was difficult to be certain of some of the characters of *Hawaiieupodes thermophilous*, such as the extent of dorso-lateral compression, due to the type material being permanently mounted, while other features could not be discerned at all. In the absence of improved data, *Hawaiieupodes* is retained as a monotypic genus.

The genus *Cocceupodes* can be easily recognised by the location of the internal vertical setae posterior to the naso. It is, however, a comparatively heterogeneous taxon with variation seen in form of internal vertical setae and number of setae associated with the genitalia, features constant in the majority of genera. At present, the number of species that would fall into the different subgroups, even taking into account the

taxa not included in this study, is regarded to be too small to justify subdivision but, as other species are discovered, a split may be warranted.

Despite Strandtmann's opinion that its species are large examples of *Eupodes* (Strandtmann 1970), the genus *Linopodes* is retained. Apart from the conspicuously long and slender first pair of legs, members can be shown to differ from species of *Eupodes* in a number of aspects, such as the body form and the number of coxae and pseudanal setae, and to have a closer affinity to *Cocceupodes*.

Penthaleus, *Linopenthaloides* and *Halotydeus*, the three genera into which the family Penthaleidae is traditionally divided, are perpetuated. Strandtmann (1981) includes the genus *Linopenthaleus* Willmann in his key to the Penthaleidae. This genus was diagnosed on the basis of leg lengths, a feature that is very variable in the species of the genus *Penthaleus* and so *Linopenthaleus* is here regarded as a *nomen nudum*.

Penthalodes and *Stereotydeus*, the two genera conventionally classified in the family Penthalodidae were clearly defined in analyses. Several interesting new characters were identified, in particular, the presence of distal genual papillae on the legs, a feature shared with the members of the family Penthaleidae.

In the family Rhagidiidae, the genera *Coccorhagidia* and *Rhagidia* are essentially returned to their original concepts. Although, in this form, the latter is a large and somewhat heterogeneous group, it is believed that species are more easily identified than when, as is the case in the classification of Zacharda (1980), species are divided into small genera and subgenera. Zacharda's monograph on the Rhagidiidae is the most thorough work that has been carried out on the family and has had the

most radical affect on the classification (Zacharda 1980). As such, it requires a detailed assessment:

Zacharda's rationale for carrying out his detailed study of the family was to organise the 'heterogeneous intricate species into a new generic classification to facilitate specific identification'. The generic classification is stated to be based on 'mostly phylogenetic evaluation of external morphology', combinations of adaptive, synapomorphic, edaphomorphic and troglomorphic characters plus the morphology of the mouthparts being used for generic diagnoses. Although Zacharda, thereby, suggests he is producing a phylogenetic analysis, his methodology is not specified and is not cladistic, despite the utilization of cladistic terminology. He, for example, does not determine apomorphic characters by out-group comparison or any of the other methods normally used (see section 8.3), nor does he establish the Rhagidiidae as a holophyletic group nor determine its sister-group. Instead, he lists plesiomorphic characters based on the assumptions of acarine primitiveness given in van der Hammen (1969). Although Zacharda lists these characters under the heading of 'Plesiomorphic', some of them he notates as being derivative and none were found, in this study, to be diagnostic of genera. Zacharda bases his view of the apomorphic state largely on ecological assumptions and applies new terms to describe them. He assumes rhagidiids to be primitively surface or near-surface soil inhabitants (hemi-edaphons), which can be, secondarily, strikingly morphologically adapted to life deeper within the soil or in caves. He, therefore, interprets and equates apomorphic characters to adaptations to special environments, a concept more in tune with the school of evolutionary biology. Thus, special morphological adaptations to a 'genuine' troglobitic life style, *i.e.* as seen in those species restricted to the

cave environment, are termed 'troglomorphisms' and those to a deep soil environment in euedaphic species, 'edaphomorphisms'. The morphology of the mouthparts is also regarded to be adaptive and Zacharda bases his interpretation of form versus the type of food taken on Karg's (1962) work on the Mesostigmata.

Troglomorphisms include the absence of eyes and pigmentation and the possession of capitate setae, expanded rhagidial organs, elongated legs, palps and chela and the duplication of rhagidial organs.

Euedaphic species prefer to live in deeper soil levels and are said to be conspicuously morphologically adapted to life. Compared with surface-dwellers, which Zacharda considers show no special morphological adaptation, they are small, desclerotized and not pigmented, the eyes are more or less reduced or absent while the rhagidial organs are well-developed and structurally complicated. As Zacharda points out, these resemble troglomorphisms and are attributed to the comparable conditions in the two environments, such as absence of light and high moisture content of the air. The following are given as distinguishing features of euedaphons - small body, short appendages and setae and usually a relatively small number of setae.

The hemiedaphic representatives are said to be more heavily sclerotized, mostly pigmented and to possess eyes, medium-lengthed appendages, slender palp tibiotarsus, leg tarsi and empodia, three or four rhagidial organs oblique or in tandem and sharply pointed setae, not reduced in length or number. Zacharda points out, however, that the types of characters identified above are not exclusive to each habitat category and that overlap often occurs. In all the characters he quotes, there are no major discontinuities, for example, palp tibiotarsal length ranges from 1.4 to five times the width, and this gradation of character state

undermines his basis for establishing apomorphies. In addition, many of his supra-specific taxa have a small number of species and this gives a limited view of habitat distribution on which to base analyses of adaptation.

The characters used by Zacharda to define genera and subgenera are not applied consistently. Numbers of rhagidial organs, coxal and genital setae are said to vary, while much importance is bestowed on the shape of the chelicerae which, although it does vary, is not always comparable in his descriptions. For example, a 'distinct saddle-shaped depression' in the dorsum of the chelicerae pertains to a number of different forms. Furthermore, the species classified in a particular genus do not always agree with the descriptions given, for example, compare the members of the following two:

***Robustocheles*:** 'Cheliceral shears robust, digitus fixus with flattened inner margin which can be sometimes reduced to large prebasal thorn pointed forward. Dorsum of chelicera convex with distinct saddle-shaped depression. Distal cheliceral seta inserted dorsally or almost dorsally but never in longitudinal, proximally open dorsolateral depression. Terminal palpal segment with relatively short and thick setae. Rhagidial organs I and II consists of 4 and 3 rhagidial setae respectively. Epimeral formula 3-1-5-3 or 3-1-6-3.'

***Rhagidia*:** 'Dorsum of chelicerae convex, with distal saddle-shaped depression, cheliceral shears slender. Digitus fixus without any thorn on its inner margin; but often broaden just before its basis. Cheliceral setae inserted dorsally. Trichobothria filiform. Rhagidial organ I consists of 4 oblique rhagidial organs. Rhagidial organ II consists of 2-4 rhagidial setae. Epimeral formula 3-1-5-3 or 3-1-6-3. No distinct troglomorphisms or edaphomorphisms'.

In the case of the members of the genus *Robustocheles*, the chelicerae show as much variation between each other as between themselves and the chelicerae of other genera. The solenidial complement and arrangement, especially on tarsus I, is also very variable within the genus. The palp tibiotarsus of *R. mucronata* is relatively short and robust whereas that of *R. montana* is long and slender. A similar variability is seen in *Rhagidia*; *R. gelida* is unusual in possessing a 'heeled' palp tibiotarsus (a feature it shares with *Brevipalpia minima*), which Zacharda does not remark upon. The chela of *R. gerlachei* account for half the length of the chelicera. The rhagidial organs of tarsus I are hardly oblique, while the fixed digit is like that of *Robustocheles*.

In another example, the genus *Parallelorhagidia*, the two member species have a different cheliceral form. The chela of *P. evansi* account for about a third of the cheliceral length, in *P. hawaiiensis*, for only about a quarter, while *cha* is, respectively, located proximal to and on the fixed digit. Furthermore, the setal complements of the coxae and of the genital area differ.

In the present study, expanded trichobothria are regarded to be consistent within genera but, in a number of Zacharda's genera (*Arctorhagidia*, *Poecilophysis*, *Tuberostoma*), the form varies. *A. mariehammerae*, for example, possesses filiform trichobothria whereas, in *A. sateri* the trichobothria are clavate.

As a consequence of the analyses, only the genera *Rhagidia*, *Coccorhagidia*, *Latoempodia*, *Shibaia* and *Trochlocheles* are retained. Whilst the results indicated the invalidity of many of Zacharda's genera

and subgenera, they did not resolve all of the problems associated with the systematics of the family Rhagidiidae. However, until a better solution is found, it is felt that the classification proposed here permits both the identification of specimens and the accommodation of new information to be more easily effected.

9.3 TAXONOMIC SUMMARY

1. The superfamily is divided into four families the Eupodidae, Penthaleidae, Penthaleodidae and Rhagidiidae.
2. The monotypic family Strandtmanniidae Zacharda is not recognised, its two member species being classified in the Rhagidiidae.
3. Fain's subdivision of the family into the subfamilies Eupodinae and Bencinyssinae is not supported (Fain 1958).
4. In the family Eupodidae, the genera *Cocceupodes*, *Linopodes*, *Claveupodes* and *Hawaiieupodes* are retained.
5. With the establishment of an amended definition for *Eupodes*, a number of the species previously classified in this genus are transferred to others.
6. The genus *Bencinyssus* is recognised and its membership increased by two, both of these species being transferred from *Eupodes*.
7. The monotypic genus *Egypteupodes* is not recognised and *E. strandtmanni* is transferred to *Eupodes*.
8. The genera *Alloepodes*, *Aneboepodes*, *Caleupodes* and *Subeupodes* are erected. The members of *Alloepodes* and *Subeupodes* comprise those species which were previously classified in the now invalid genus *Prottereunetes*.

9. The genus *Hawaiieupodes* is retained for the present, but with some reservations in the absence of more complete morphological data.
10. Strandtmann (1970) puts forward the opinion that species of *Linopodes* could be considered to be large examples of *Eupodes*. This view is not supported since *Linopodes* is shown to have a closer affinity with *Cocceupodes*.
11. The three genera traditionally classified in the family Penthaleidae are retained. These are *Halotydeus*, *Penthaleus* and *Linopenthaloides*, the genus *Linopenthaleus* Willmann being declared invalid.
12. The generic membership of the family Penthalodidae is unchanged and comprises *Penthalodes* and *Stereotydeus*.
13. The number of genera in the family Rhagidiidae is much reduced, but it is accepted that the systematics of the family is still not satisfactorily resolved.
14. Sixteen of the supra-specific taxa erected by Zacharda (1980) are considered invalid because they are insufficiently diagnosed and based on subjective characters. They are:- *Arctorhagidia*, *Brevipalpia*, *Crassocheles*, *Elliotta*, *Eskimaia*, *Evadorhagidia*, *Flabellorhagidia*, *Foveacheles*, *Hammenia*, *Parallelorhagidia*, *Poecilophysis*, *Rhagidia* (*Noerneria*), *Robustocheles*, *Thoria*, *Traegaardhia* and *Tuberostoma*.
15. The rhagidiid genera *Rhagidia*, *Coccorhagidia*, *Latoempodia*, *Pilorhagidia*, *Shibaia* and *Troglocheles* are recognised.
16. The genus *Rhagidia* is essentially returned to its original concept. It, therefore, remains a rather large and heterogeneous group, but, despite this, it is believed that species identification is more easily achieved.
17. *Coccorhagidia* is also largely returned to the original concept of the genus, i.e. rhagidiids with expanded trichobothria, but with the additional qualifying feature of possessing a holotrichous chaetome.

SYSTEMATIC STUDIES ON MITES OF THE SUPERFAMILY EUPODOIDEA
(ACARI: ACARIFORMES) BASED ON THE FAUNA OF THE BRITISH ISLES

Volume 2

by

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10. DESCRIPTION OF THE TAXA

The 40 species collected during the course of this study are listed in Table 10. Descriptions of the members of supra-specific taxa are so arranged that the type, when present, comes first, followed by the remainder in alphabetical order.

For the most part, descriptions are based on ten cleared female specimens, preferably, from the same population. If this was not possible, examples from a number of localities were used. When fewer than ten specimens had been found, the number is stated at the beginning of the definition. Since sexual dimorphism is only evident in the genital area, details of male specimens are limited to the form of the sperm sac.

The description of each taxon begins with a list of synonymies, which cites the major sources of reference. These include the original description, synonymous names, misidentifications and confirmation of identifications. This is followed by a diagnosis which gives the features which distinguish the taxon from, unless indicated otherwise, all others, and a definition which gives a general account of characteristics. Etymology is given for new taxa.

Distribution data are given after each description. Locality and habitat details of the specimens on which specific descriptions are based, including type material, appear in a 'Material examined' section, while other British records are listed subsequently. Unless a limited occurrence is indicated, species were found in many samples and so representative localities and habitats only are listed. Collectors of material, other than the author, are given in brackets after the sample details. A concluding remarks section discusses any items of interest.

Table 10. The eupodoid fauna of the British Isles.

Names in brackets after certain species are references used in systematic analyses (section 8.3), * = new record.

Family Eupodidae Koch

Genus *Eupodes* Koch*E. abbreviatus* n.sp. (*Eupodes* 1)*E. alaskanensis* Strandtmann **E. striatus* n.sp. (*Eupodes* 3)*E. truncatus* n.sp. (*Eupodes* 2)Genus *Alloeupodes* n.gen.*A. interruptus* n.sp. (*Eupodes* 9)Genus *Aneboeupodes* n.gen.*A. minimus* n.sp. (*Eupodes* 8)*A. magnus* n.sp. (*Eupodes* 13)Genus *Benoinyssus* Fain*B. najae* Fain **B. ereynetoides* (Strandtmann & Prasse) **B. momeni* (Abou-Awad) *Genus *Caleupodes* n.gen.*C. reticulatus* n.sp.Genus *Claveupodes* Strandtmann & Prasse*C. delicatus* Strandtmann & Prasse **C. juvenalis* n.sp. (*Claveupodes* 2)*C. ornatus* n.sp. (*Claveupodes* 3)Genus *Cocceupodes* Thor*C. australis* Strandtmann & Prasse **C. breweri* Strandtmann **C. minutus* n.sp. (*Cocceupodes* 4)*C. paradoxus* Weis-Fogh*C. setosus* Evans*C. stellatus* Strandtmann & Prasse **C. trisetatus* Strandtmann & Prasse *Genus *Linopodes* Koch*L. agitatorius* Berlese **L. motatorius* (L.)Genus *Subeupodes* n.gen.*S. boernerii* (Thor) (*Eupodes* 11)

Family Penthaleidae Oudemans

Genus *Penthaleus* Koch*P. longipilis* (Canestrini)*P. minor* (Canestrini) *

Family Penthaleodidae Thor

Genus *Penthaleodes* Murray*P. ovalis* (Dugès)*P. nitidus* (Berlese) *

Family Rhagidiidae Oudemans

Genus *Rhagidia* Thorell*R. arena* Zacharda **R. clavicrinita* Ehrnsberger **R. montana* Zacharda **R. punkva* Zacharda **R. spalaea* (Wankel)Genus *Coccorhagidia* Thor*C. clavifrons* (Canestrini)*C. evansi* Strandtmann & Prasse **C. pittardi* Strandtmann **C. subteranea* (Berlese)Genus *Latoempodia* Zacharda*L. macroempodiata* Zacharda *Genus *Shibaia* Zacharda*S. heteropoda* (Berlese) *

Measurements and setal formulae

All measurements (demonstrated in Fig. 47) are made on specimens temporarily mounted in lactic acid in cavity slides. This has the advantage of minimizing distortion by flattening, as occurs in permanently mounted specimens, but the disadvantage of allowing setal curvature, so making measurement difficult. The latter was overcome by orientating the specimen so that all of the seta was in focus, drawing it with a map measurer and extrapolating the length.

Dimensions are given in microns (μm), those of most structures are given as a mean followed by the range in brackets although, where little variation can be measured, only the mean or the range is given.

The various setal formulae given in descriptions should be interpreted as follows:

Coxae	I-II-III-IV
Palp	femur-genu-tibiotarsus
Leg	trochanter-femur(basi- + telofemur)-genu-tibia-tarsus

Depositories of material examined

Non-type material collected in the British Isles is housed in the British Museum (Natural History). The depository of other specimens is given in square brackets after collection data and are abbreviated as follows:

BM - Bishop Museum, Honolulu.
 BMNH - British Museum (Natural History), London.
 ISZA - Istituto Sperimentale per la Zoologia Agraria, Florence
 MLU - Martin-Luther Universität, Halle-Wittenberg.
 MRAC - Musée Royal de l'Afrique Centrale, Tervuren.
 MZ - M. Zacharda Coll., Institute of Entomology, Budejovice.
 PPL - Plant Protection Laboratory, Cairo.
 UO - Universität Osnabrück.

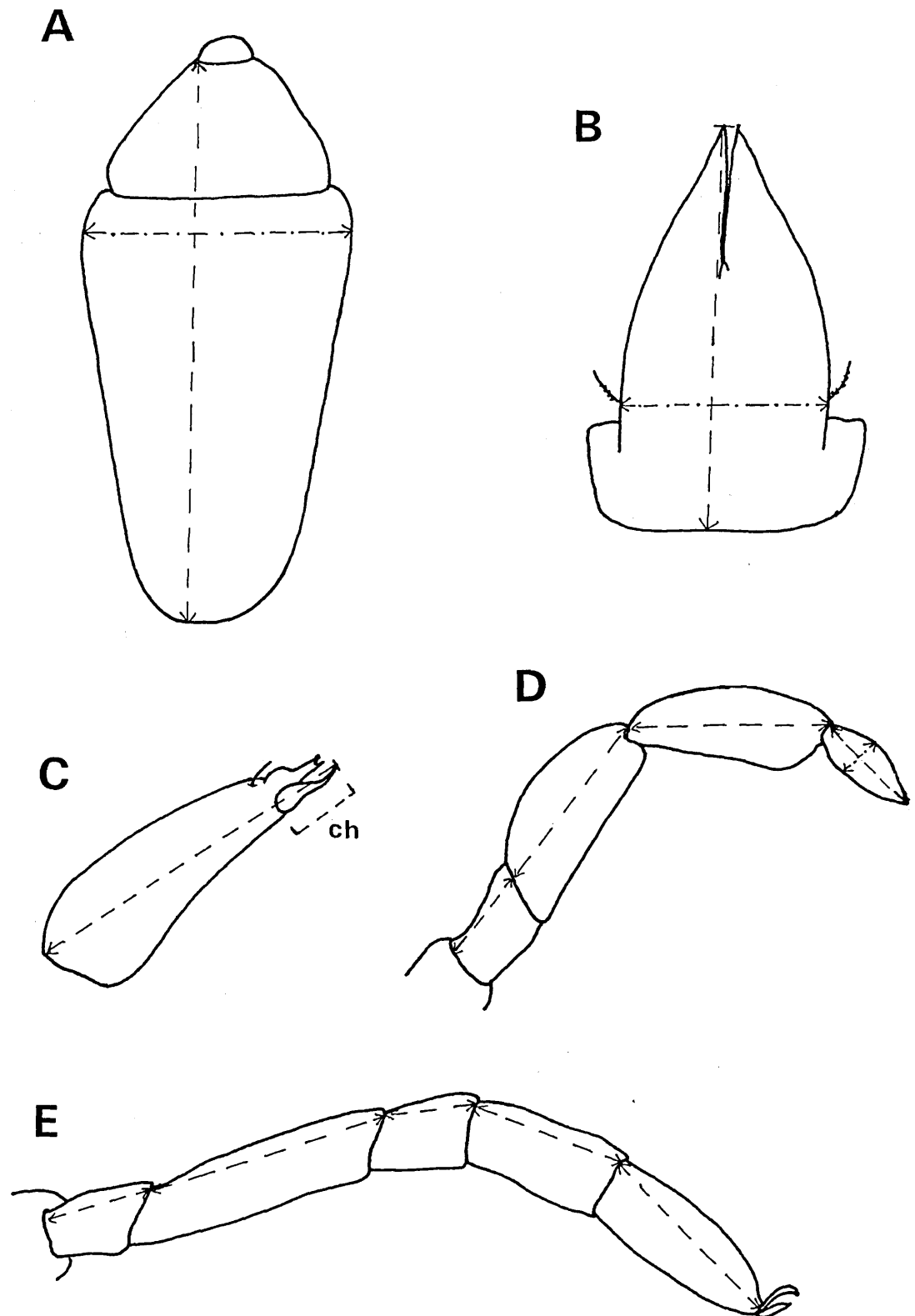


Fig. 47. Demonstration of measurement of body and appendages:

(A) idiosoma; (B) subcapitulum; (C) chelicera, ch=chela;
 (D) palp; (E) leg.

← - - → length, ← - - - → width/breadth.

10.1 SUPERFAMILY EUPODOIDEA BANKS

Eupodoidea Banks, 1894: 209 [in part]. Cunliffe, 1955: 5. Krantz, 1978: 235. Livshits & Mitrofanov, 1978: 109. Zacharda, 1979: 77. Kethley, 1982: 121.

DIAGNOSIS. Members of the superfamily are distinguished from other mites by the presence anteriorly on the prodorsum of a more or less delimited lobe, the naso, and by recumbent solenidia (rhagidial organs) on at least tarsi I and II.

DEFINITION.

Small to large (170-2000 long), mostly soft-bodied mites.

Integument of idiosoma generally weakly striate-spiculate or papillate, sometimes reticulate; prodorsal shield of differentiated integument usually present; appendages spiculate or papillate, sometimes reticulate. Chaetome holotrichous, sometimes neo- or hypotrichous; setae normally simple and ornamented.

Opisthosomal segments: seven.

GNATHOSOMA.

Subcapitulum with two pairs, usually ornamented, setae inserted laterally (subcapitular seta, sbc_1) and ventrally (subcapitular seta, sbc_2) and, apically, two, rarely one, pairs smooth adoral setae (or_1 & 2) ranging from minute and difficult to discern to long and conspicuous.

Palp: simple with four free segments; one pair minute supracoxal setae usually present; trochanter devoid of setae; femur with two, rarely one, setae, genu with three, rarely one or two, setae; tibiotalpus with nine to 14 setae usually with either a rhagidial organ or spiniform solenidion.

Chelicera: independent, somewhat variable; main body either long and slender or robust; chela smooth, weakly or strongly chelate or fixed digit

reduced and drawn into finger-like processes; one or two setae located just proximal to and/or on fixed digit, rarely, chelicerae devoid of setae.

IDIOSOMA - DORSUM

Scutal furrow normally clearly subdivides idiosoma into prodorsum and opisthosoma; sometimes represented only by faint line of differentiated integument and body not subdivided; rarely, furrow absent.

Naso ranges from small extension of prodorsum to conspicuous, clearly delimited lobe.

Eyes sometimes present located by scapular setae; if present, either visible only in cleared specimens as dark granular subcutaneous area or are raised, dome-like structures.

Setae: four, rarely three or five, pairs prodorsal setae; anterior pair (*iv*), when present, trichobothridial, located either on or at base of naso and simple or just posterior to it and simple to capitate; one median pair of trichobothria (*T*), ranging from filiform to capitate; holotrichous chaetome comprises eight pairs opisthodorsal setae arranged in five rows on, respectively, segments C to H, (*f₂*) or (*h₁ & 2*) absent in certain taxa; rarely, (*f₁*) trichobothridial, like filiform (*T*) or with enlarged bases and seta normal.

Lyrifissures: three pairs located on, respectively, segments D to F.

IDIOSOMA - VENTER

Podosoma: coxae fused to ventral body wall, delimitation ranges from complete to only distal limits clear; on either side of body, adjacent margins of coxae I and II and of III and IV contiguous, proximal limits of pairs sometimes meet but never fuse; I and II with respectively three and one setae, III with three to seven, IV with three, rarely, two or four; where coxae incompletely defined, proximal setae of I, II and IV inserted outside coxal limits but still on coxal integument.

Genital area surrounded by variable number of eugenital setae, often mounted on small tubercles; two pairs genital papillae; two genital shields cover this area, usually roughly kidney-shaped with outer margins faintly defined, sometimes rounded rectangular and clearly delimited; variable number of genital setae usually in single file along free edge of shields, sometimes with one or more lateral to others; variable number of aggenital setae encircle shields.

Sexual dimorphism only evident in genital region, genital shields of males being ca. two-thirds size of those of respective female, while eugenital setae shorter and more tightly clustered round genital aperture; female with ovipositor, ranging from simple evagination of internal genital membrane to differentiated tube bearing rings of eugenital setae; male with simple accessory glands and subclavate to capitate, variously sclerotized, sperm sac leading from aperture.

Anal region: anus opens onto adanal segment (AD), slit-like and flanked by two flaps or circular and collar-like; usually subterminal or terminal, rarely dorsal; flaps devoid of setae or with one pair of adanals; with two to three pairs pseudanal setae and one pair lyrifissures ventrally on H segment.

LEGS.

Generally long and slender although femur IV sometimes conspicuously enlarged; supracoxal seta I present, of similar form to that of palp; femoral subdivision ranges from absent to complete; all tarsi terminate in an apotele comprising two lateral rayed claws flanking pad-like empodium of similar length; certain solenidia, on at least tarsi I and II, recumbent or semi-erect in pits (rhagidial organs); tarsus I with famulus comprising a central mushroom-shaped part surrounded by a number of finger-like processes; tarsus II normally with spiniform famulus; famulus

of tibia I present or absent; other solenidia long and blunt or short and spiniform.

DEVELOPMENT.

Life stages: egg, inactive prelarva, active larva, proto-, deuto-, tritonymph and adult.

Sperm transfer by spermatophores, although parthenogenesis demonstrated in certain species (Ehrnsberger 1977a).

DISTRIBUTION. Cosmopolitan.

REMARKS. Until recently, the diagnosis for the superfamily Eupodoidea included the presence of a pair of setae, the internal verticals, associated with the naso. However, the discovery of *Eupodes strandtmanni* (Abou-Awad), which lacks internal vertical setae, has caused me to amend the diagnosis accordingly. Similarly, the establishment of the trichobothridial state of the internal verticals means that the definition should include the presence of two pairs, or rarely one, of prodorsal trichobothria.

Families classified in the superfamily Eupodoidea

Eupodidae Koch 1842

Penthaleidae Oudemans 1931

Penthalodidae Thor 1933

Rhagidiidae Oudemans 1922

Key to the families of the superfamily Eupodoidea

- 1 Chelicerae strongly chelate (Fig. 104D); one pair
 adanal setae; adoral setae long (Fig. 104C) RHAGIDIIDAE
- Chelicerae weakly chelate (Figs 48E & 96E); two or three pairs
 pseudanal setae or chaetome neutrichous; adoral setae
 minute (Fig. 48C) 2
- 2 Naso with associated epirostrum (Fig. 100A); dorsum with V- or
 Y-shaped furrows (Fig. 100A) or with 2 parallel longitudinal
 lines on opisthosoma PENTHALODIDAE
- Naso without associated epirostrum (Fig. 48A); dorsal furrows
 usually absent, when present, always transverse (Fig. 68A) 3
- 3 Anus subterminal, sometimes terminal; chaetome holotrichous;
 palps long and slender; subcapitular seta (*sbc*₁) and coxal seta
 (*1c*) fine and weakly ornamented (Fig. 48A-D) EUPODIDAE
- Anus dorsal, terminal or subterminal; chaetome neutrichous
 (Fig. 96A) palps short and robust (Fig. 96D); (*sbc*₁) and (*1c*)
 same form as other setae in respective area PENTHALEIDAE

10.1.1 Family Eupodidae Koch

Eupodidae Koch, 1842: 60. Thor & Willmann, 1941: 1. Baker & Wharton, 1952: 114 [in part]. Strandtmann, 1971: 77 [in part]. Wainstein, 1978:110. Kethley, 1982: 121.

DIAGNOSIS. Distinguished from other eupodoid families by the fine and weakly ornamented form of the lateral subcapitular setae (sbc_1) and distal seta of coxa I ($1c$) and the presence of two rhagidial organs on tarsus I.

DEFINITION.

Small to medium (170-700), soft-bodied mites.

Integument of idiosoma normally weakly striate-spiculate, rarely, conspicuously striate or reticulate; appendages spiculate or papillate, rarely, reticulate; differentiated prodorsal shield usually present (absent in one genus).

Chaetome: holotrichous.

GNATHOSOMA.

Subcapitulum with densely spinose subcapitular setae (sbc_2) inserted subapically to halfway along subcapitulum; weakly spiculated, fine (sbc_1) located approximately two-thirds from anterior limit, much finer than densely spinose (sbc_2); two pairs smooth minute adoral setae.

Palp: long slender, with minute supracoxal seta ornamented with papillae or spicules; femur and genu longer than broad; tibiotarsus ovoid or long and slender, with small antiaxial rhagidial organ; setal formula 2-3-9; 1' spiralled.

Chelicera with slender shaft; chela weakly chelate, edentate and small, only accounting for at most one fifth of total length; one short smooth, grooved or spinose seta, *cha*, slightly antiaxially, just proximal to chela.

IDIOSOMA - DORSUM

Sejugal furrow either well-defined, clearly dividing idiosoma into prodorsum and opisthosoma, or represented by faint line of differentiated integument not subdividing idiosoma.

Naso ranges from slight extension of prodorsum to clearly delimited lobe.

Eyes: visible in some specimens as subcutaneous granular areas.

Opisthosoma: rarely, shows evidence of primary segmentation.

Setae: (*iv*) on, at base of or just posterior to naso, or rarely absent; (*T*) filiform to clavate; (*c₂*) in line with (*c₁*) or (*T*); rarely, (*f₁*) same form as (*T*) or with enlarged, bothridial bases; in one genus (*f₂*) located just laterally and posteriorly to (*f₁*).

Lyrifissures: usually round, sometimes eye-like.

IDIOSOMA - VENTER

Podosoma: coxae generally distinctly but faintly defined, proximal margins sometimes indistinct, never meet medially; setae (*1a*), (*3a*) and (*4a*) located outside limits of margins but still on coxal-type integument; seta (*1c*) markedly finer and shorter than remainder; coxa III with three or four setae, IV with three or two.

Genital area: eugenital setae sometimes polymorphic in female; shields roughly semi-circular; genital setae arranged in single file near free edge of shields or with (*g₄*) lateral to others; ovipositor an evagination of the eugenital area; sperm sac subclavate, clavate and unornamented or reticulated and capitate.

Anal region: anus subterminal or terminal, slit-like, bounded by two flaps; two or three pairs pseudanal setae present; (*ib*) lateral and anterior to (*ps₃*).

LEGS.

Shortest just under half body length, I up to six times longer; most segments slender, sometimes femur IV conspicuously enlarged.

Solenidia & famuli: tarsi I and II with never more than respectively two and three rhagidial organs; L- or T-shaped, rarely, bridge-like with two points of attachment; famuli never elaborately developed; rarely, famulus of tarsus II absent; famulus present on tibia I; other solenidia not numerous, when present usually short and spiniform, sometimes longer and blunt.

Apotela: I sometimes reduced.

TYPE GENUS. *Eupodes* Koch

DISTRIBUTION. Cosmopolitan.

Genera classified in the family Eupodidae

Eupodes Koch 1835

Allaeupodes n.gen.

Aneboeupodes n.gen.

Benoinyssus Fain 1958

Claveupodes Strandtmann & Prasse 1976

Caleupodes n.gen.

Cocceupodes Thor 1934

Hawaiieupodes Strandtmann & Goff 1978

Linopodes Koch 1835

Subeupodes n.gen.

Key to the genera of the family Rupodidae

- 1 Leg I markedly more slender than other legs, more than three times body length; sejugal furrow indistinct; (g_4) lateral to other genital setae; two pairs pseudanal setae; femur IV not greatly enlarged (Figs 90 & 91) *Linopodes*
- Leg I of similar form to other legs, less than twice body length; sejugal furrow distinct or indistinct; (g_4) lateral to or in line with other genital setae; two or three pairs pseudanal setae; femur IV enlarged or slender 2
- 2 Internal verticals (iv) located posteriorly to naso (Fig. 76A); two pairs pseudanal setae; trichobothria (T) filiform *Cocceupodes*
- (iv) absent or located at base of or on naso; two or three pairs pseudanal setae; (T) subclavate, clavate or filiform 3
- 3 (iv) located at base of naso; (T) subclavate or clavate; (f_2) setae just lateral and posterior to (f_1) (Fig. 70A) *Claveupodes*
- (iv) on naso or absent; (T) filiform; (f_2) approximately in line with (f_1) (Fig. 48A) 4
- 4 Body laterally compressed; three setae on coxa III ** Hawaiiupodes*
- Body dorso-ventrally compressed; four setae on coxa III 5
- 5 With two pairs pseudanal setae 6
- With three pairs pseudanal setae 7

- 6 Integument with reticulate ornamentation; opisthosoma with transverse furrows of differentiated integument denoting segments (Fig. 68A); (*f*₁) with normal base; coxal seta (*4c*) present *Caleupodes* n.gen.
- Integument striate; opisthosoma without external evidence of segmentation; (*f*₁) with enlarged, bothridial base (Fig. 58A); (*4c*) absent (Fig. 58B); *Aneboeupodes* n.gen.
- 7 (*f*₁) trichobothridial (Fig. 62A) *Benoinyssus*
- (*f*₁) setiform (Fig. 48A) 8
- 8 Proximal solenidion of tibiae I & II spiniform (Figs 49A-D); leg I as long as or longer than body; femur IV conspicuously enlarged (Fig. 49F); two rhagidial organs on tarsus II *Eupodes*
- Proximal solenidion of tibiae I & II rhagidiform (Figs 57A-D); leg I clearly shorter than body; femur IV slender; two or three rhagidial organs on tarsus II 9
- 9 Three rhagidial organs on tarsus II (Fig. 95B) *Alloeupodes* n.gen.
- Two rhagidial organs on tarsus II (Fig. 57B) *Subeupodes* n.gen.

* Genus not recorded from the British fauna

10.1.1.1 Genus *Eupodes* Koch

Eupodes Koch, 1835: 18. Thor & Willmann, 1941: 5. Strandtmann, 1970: 89
[in part]. Strandtmann, 1971: 78.

DIAGNOSIS. Distinguished from other eupodid genera by the female possessing heteromorphous eugenital setae and both sexes with the combination of four setae on coxa III, three pairs of pseudanal setae, the position of (g_4) lateral to the other genital setae and the usually enlarged femora IV.

DEFINITION. Small to medium (290-650 long).

Integument of idiosoma weakly striate-spiculate; prodorsal shield with more densely spiculed striae than surrounding integument; appendages spiculate or papillate.

GNATHOSOMA.

Subcapitulum: ratio length to width ca. 1:0.6; (sbc_1) markedly shorter than (sbc_2), inserted subapically to mid-way between (sbc_1) and anterior limit of subcapitulum.

Palp: with slender, tapering tibiotarsus, length ca. three times greatest width.

Chelicera: chela account for approximately one fifth of total length; fixed digit terminates in shallow fork; movable digit narrows to slender part in distal third; *cha* smooth.

IDIOSOMA - DORSUM

Seiugal furrow clearly subdivides idiosoma into roughly triangular prodorsum and opisthosoma with shoulders narrowing to rounded posterior. Naso a clearly delimited lobe, with separating suture.

Setae: (iv) located on naso; (sc) and (c_2) more robust than others; (ev) located mid-way between (T) and anterior margin of prodorsum; (sc) in

line with (T) but markedly lateral to them; c row in line, approximately level with shoulders; f and h rows close to posterior limit of opisthosoma; relatively long, approximately half distance to or overlapping base of posterior seta; (T) filiform, spiculated, markedly so along distal two-thirds; other setae densely spinose, simple.

Lyrifissures: circular.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-3; densely spinose setae blunt or spatulate.

Genital area with six pairs tapering densely spiculated eugenital setae, polymorphic in female, (eu_3 & 4) being clavate; six pairs genital setae, with (g_4) lateral, and five or seven pairs aggenitals, all densely spinose, more or less spatulate; males with clavate and unornamented or capitate and reticulated sperm sac.

Anal region: anus subterminal or rarely terminal; three pairs of pseudanal setae, (ps_3) always shorter than others; ih lateral and anterior to (ps_3).

LEGS.

Femora IV moderately to greatly enlarged although rarely slender, other segments slender; legs I approximately equal to or longer than body length.

Setae densely spiculated to spinose; complement variable.

Solenidia & famuli: rhagidial organs L-shaped; tarsi I and II both with two rhagidial organs (ω_1 & 2) in tandem and in confluent pits, those of I located in distal half of segment, those of II in median third; famuli just posterolateral to base of ω_1 ; tibia I with (k) distally and slightly posterolaterally, with or without associated rhagidial organ, plus spiniform solenidion dorsoproximally; tibia II with distal rhagidial organ

plus dorso-proximal spiniform solenidion; genu I sometimes with dorsobasal spiniform solenidion.

Apotela: all of similar form.

TYPE SPECIES. *E. striola* C. L. Koch 1835 [here designated]

DISTRIBUTION. Cosmopolitan.

REMARKS. Traditionally, the date of establishment of the genus *Eupodes* is given as 1836 while the type species is quoted as being *E. hiemalis* Koch 1836. However, referral to Sherborn's list of publication dates for the 'Hefte' of Koch's *Deutschlands Crustaceen, Myriapoden und Arachniden* shows that the respective dates of these taxa should be 1835 and 1838 (Sherborn 1923). Furthermore, under the rules of the International Code of Zoological Nomenclature (1985), *E. hiemalis* is ineligible to be the type species of the genus. The assumption of its status apparently arose due to Koch listing it separately in his subsequent account of *Eupodes* (Koch 1842). The generic name first appeared in 1835 when Koch described the species *E. striola* and *E. signatus*, but he did not designate a type species. *Eupodes* is therefore available by indication (Article 12(b)(5)) and the type must be one of these original two species (Article 69(a)). Consequently, I have designated the species which appears first, *i.e.* *E. striola*, as type. Despite Koch's cursory description of *E. striola*, his figure clearly indicates that the concept of *Eupodes* described here, and indeed that existed before Fain's invalidation of the genus *Prottereunetes* (Fain 1964), conforms to Koch's concept of the genus.

Two species groups are suggested within *Eupodes*, one in which five pairs of aggenital setae occur and a rhagidial organ is associated with

the famulus of tibia I and another with seven pairs of aggenital setae and the famulus occurring alone. To date, it has been possible to assign *E. angardi*, *E. hawaiiensis*, *E. strandtmanni*, *E. tottanfjella*, *E. wisei* and *E. wisnesi* to the first group while all of the species found in Britain (see below) belong to the second.

Five species of *Eupodes* have been recorded from the British Isles: *E. variegatus* Koch (Hull 1918, Halbert 1915, Luxton 1967, Hazelton 1970); *E. unifasciatus* Koch (Turk & Turk 1952, Hazelton 1970); *E. skiaaki* Thor (Evans 1954, Turk 1972, Hazelton 1970); *E. voxencollis* Thor (Evans 1952); *E. vallambrosae* Thor (Hazelton 1970, Turk 1972). I consider all of these species, however, to be *species inquirendae* since they have not been described in sufficient detail to allow identification and type material does not exist to clarify their identities.

Key to the British species of *Eupodes*

1. Anus terminal, visible in dorsal view; idiosoma with
conspicuous lateral bands of striae *E. striatus* n.sp.
- Anus subterminal, not visible in dorsal view; idiosomal
ornamentation inconspicuous 2
2. Proximal rhagidial organ of tarsus I twice length of distal
E. abbreviatus n.sp.
- Rhagidial organs of tarsus I subequal 3
3. Idiosomal setae short, extending ca. half distance to base
of posterior; sejugal furrow relatively indistinct;
tarsus I with 22 setae *E. truncatus* n.sp.
- Idiosomal setae long, easily overlapping base of posterior;
sejugal furrow distinct; tarsus I with 28 setae
E. alaskanensis

Eupodes abbreviatus n.sp.

Figs 48 & 49

DIAGNOSIS. This species can be distinguished from other members of *Eupodes* by the relatively short legs and idiosomal setae, the proximal rhagidial organ on tarsus I being twice the length of the distal and by the leg chaetotaxy.

Body length 391 (383-400), width 199 (194-207) (5 specimens examined).

GNATHOSOMA (Figs 48C,D,E)

Subcapitulum: (sbc_2) ca. 11 long, inserted approximately two-thirds distance from (sbc_1), ca. 4 long, and anterior limit of subcapitulum.

Palp: typical for genus.

Chelicera: total length 87 (85-91); *cha* 8.

IDIOSOMA - DORSUM (Fig. 48A)

Eyes: observed in some specimens as dark, roughly circular, granular areas.

Setae: rather short, not reaching base of following seta; lengths - (*iv*) 17 (15-19), (*ev*) 29 (26-32), (*T*) 62 (57-64), (*sc*) 29 (26-33), (c_2) 57 (54-61), (c_1), (d_1) and (e_1) subequal ca. 36, (f_1) 41 (38-45), (f_2) 34 (31-38), (h_1) 49 (46-53), (h_2) 36 (33-38).

IDIOSOMA - VENTER (Figs 48B,F)

Podosoma: (*a*) and (*b*) setae spatulate, remainder blunt; lengths - (*1a*) 24, (*1b*) 29, (*1c*) 13; (*2b*) 31; (*3a*) 17, (*3b-d*) subequal ca. 21; (*4a*) 13, just over half length of subequal (*4b & c*).

Genital area: ($eu_{1,2,5,6}$) approximately 17 long, approximately twice length of clavate (eu_3 & 4); (g_4) at 13, slightly longer than other subequal

genital setae, ca. 11 long; seven pairs aggenital setae, decrease in length posteriorly from ca. 17 to 13.

Anal region: (ps_1) 41(38-44), (ps_3) 16 long, just over half length of (ps_2).

LEGS (Fig. 49)

I approximately body length, II and III approximately half, IV just over three-quarters body length.

Setae: formulae I 1-20(14+6)-12-14-22, II 1-14(9+5)-9-9-16, III 1-8(4+4)-5-6-15, IV 1-7(4+3)-4-5-14.

Solenidia & famuli: proximal rhagidial organ of tarsus I approximately twice the length of the distal; tibia I lacks distal rhagidial organ.

MALE. Unknown.

ETYMOLOGY. The specific name refers to the rather short legs and setae.

DISTRIBUTION. England.

MATERIAL EXAMINED. Type material: Holotype ♀, ENGLAND, Essex, Colne Point Nature Reserve, approx. 500m south of North Mud Flats and 30m inland from North Horse Wash inlet, along *Sueda* path, from 3cm deep layer of soil under sea purslane (*Halimione portulacoides*), 12.v.1981 [BMNH, reg.no. 1987.3.23.11]. Paratypes 4 ♀♀, same data as holotype [BMNH, reg.nos 1987.3.23.2-5].

REMARKS. This was the rarest of the *Eupodes* species, found only from the type locality.

Fig. 48. *Eupodes abbreviatus* n.sp.:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial;
- (F) genital area, sagittal, ♀.

Scale intervals 10 μ m.

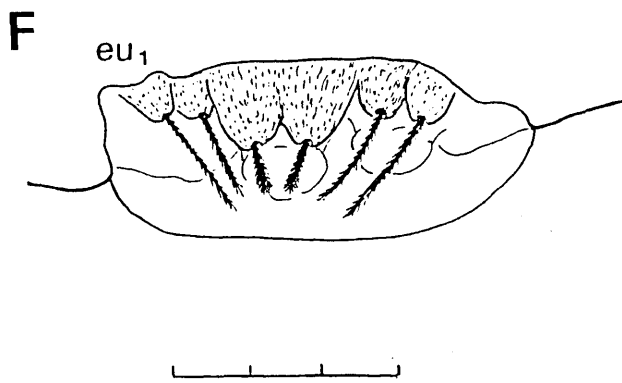
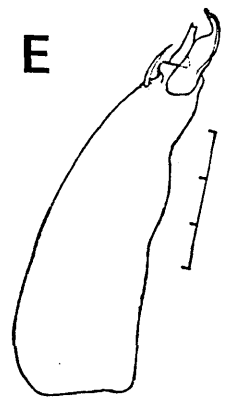
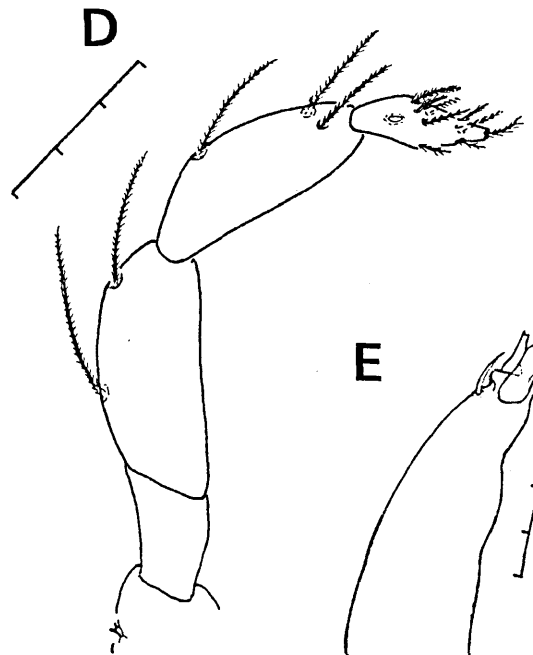
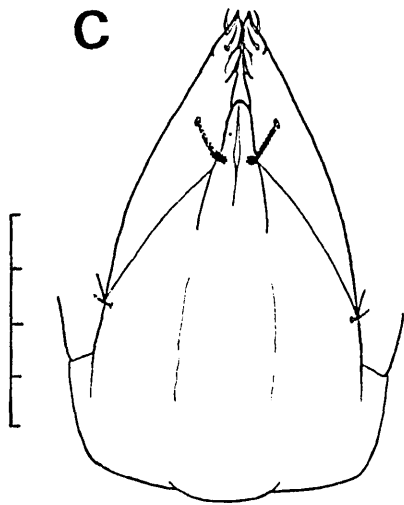
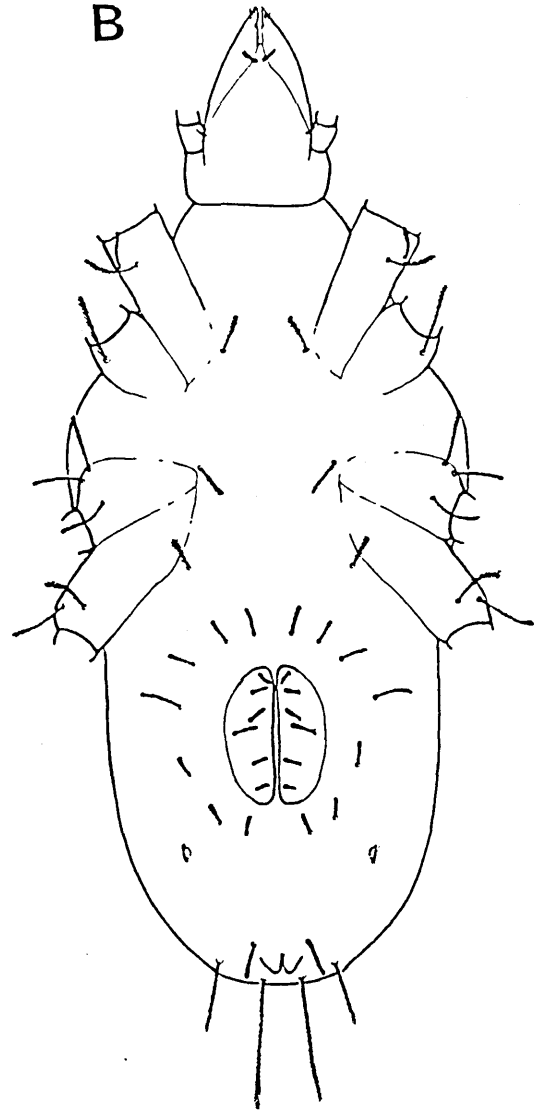
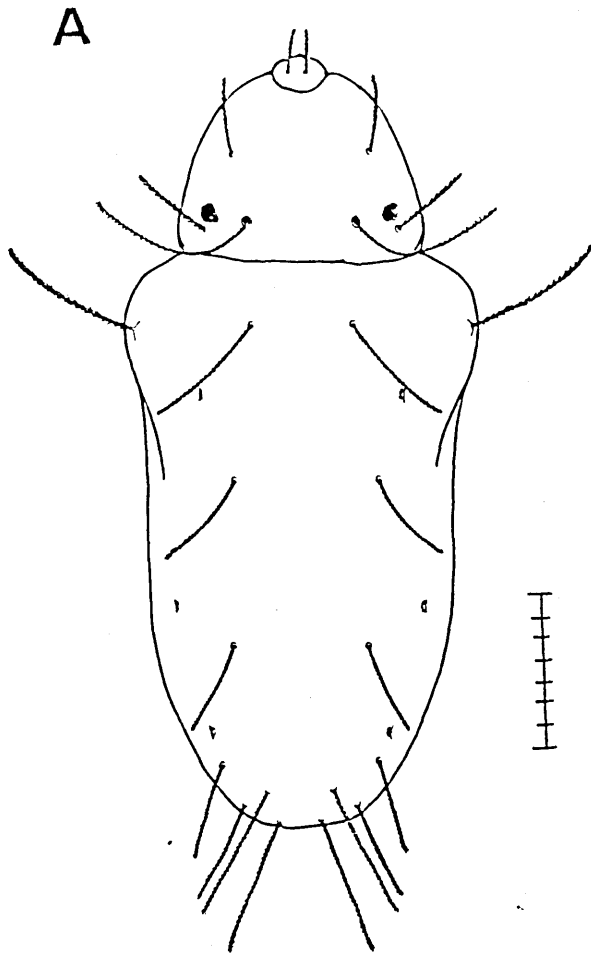
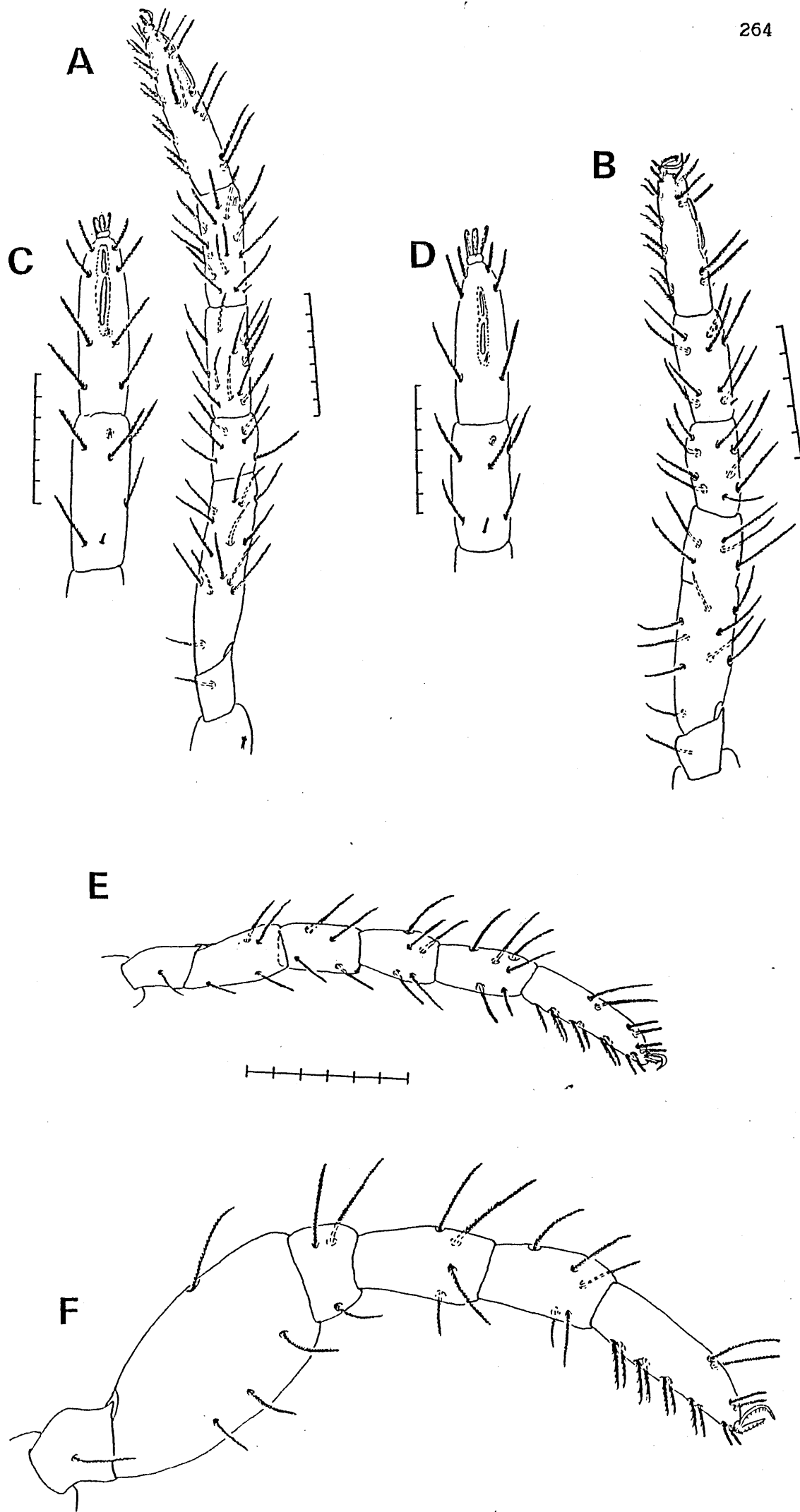


Fig. 49. *Eupodes abbreviatus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Eupodes alaskanensis Strandtmann

Figs 14a, 16b, 18a,c, 20e, 21f, 22a,d, 23d, 24d, 26, 28f, 50 & 51

Eupodes alaskanensis Strandtmann, 1971: 79.[*Eupodes acuminatus*: Strandtmann & Prasse, 1976: 4. Misidentified]New British record

DIAGNOSIS. *E. alaskanensis* can be distinguished by the long idiodorsal setae, legs I that are clearly longer than the body and by the leg chaetotaxy.

Body length 436 (419-451), width 212 (203-221).

GNATHOSOMA (Figs 22a,d, 23d, 50B)

Subcapitulum: (*sbc*₂) 9 long, inserted three-quarters of distance from (*sbc*₁), ca. 4 long.

Palp: typical for genus.Chelicera: total length 83 (78-86); *cha* 10 long.**IDIOSOMA - DORSUM** (Figs 14a, 16b, 20e, 21f, 50A)

Setae: extend past base of following seta, lengths (*iv*) 30 (26-35), (*ev*) 44 (38-49), (*T*) 88 (85-93), (*sc*) 44 (40-49), (*c*₁) 106 (101-113), (*c*₂) 79 (75-84), (*d*₁), (*e*₁) subequal 99 (103-107), (*f*₁) 86 (82-93), (*f*₂) 73 (66-78), (*h*₁) 105 (97-111), (*h*₂) 80 (76-86).

IDIOSOMA - VENTER (Figs 24d, 28f, 50B,C)

Podosoma: (*a*) and (*b*) setae spatulate, others rounded; lengths (*1a*) 35, (*1b*) 43 approximately three times length of (*1c*), (*2b*) 48, (*3a*) 39, (*3b-d*) subequal ca. 42, (*4a*) 32, (*4b* & *c*) subequal ca. 43 long.

Genital area: eugenital setae ($eu_{1,2,5,6}$) subequal ca. 20 long, densely spiculated, tapering, (eu_3 & 4) 9 long, clavate, (eu_3) particularly so; (g_4 & 5), at respectively 16 and 14, slightly longer than other genital setae, ca. 12 long; aggenital setae gradually decrease in length posteriorly from ca. 31 to 23.

Anal region: (ps_1) 55, (ps_2) 51, (ps_3) just under half length of others.

LEGS (Figs 18a,c, 26, 51)

I fifth longer than body, II just below, III just over body length, IV approximately three-quarters body length.

Setae: mostly long; formulae I 1-22(16+6)-15-17-28,

II 1-15(10+5)-7-9-16, III 1-8(4+4)-5-7-18, IV 1-7(4+3)-5-6-15.

Solenidia & famuli: typical for genus; tibia I lacks distal rhagidial organ.

MALE (Fig. 50D) (3 specimens examined). Sperm sac capitate, reticulated.

DISTRIBUTION. Eire, England, German Democratic Republic, Scotland, United States of America, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, North America, Alaska, Cape Beaufort, from moss and prostrate birch, 12.vii.1968, (R. W. & M. R. Strandtmann) [BM, slide no. 9342]. British material: ENGLAND, Devon, near Cornwood, Dartmoor, Higher piles Copse (oak wood), from moss mat, mostly *Hypnum cupressiforme*, from surface of jumbled boulders in wood 6.vi.1982 (P D Hillyard).

OTHER BRITISH RECORDS. *E. alaskanensis* was the most commonly occurring species in the British fauna, being collected throughout the country and,

apart from in caves and on the sea-shore, from all types of moist habitat.

REMARKS. Strandtmann & Prasse (1976) treated *E. alaskanensis* and *E. acuminatus* Willmann as junior synonyms of *E. voxencollinus* Thor. The assumption that *E. alaskanensis* and *E. acuminatus* are conspecific was made on the basis of Willmann's figure of a nymphal stage bearing a forked extension to the naso, a character also identified in nymphs of *E. alaskanensis*. I regard this as rather tenuous evidence since nymphs of *Eupodes* with a similar structure have been observed in samples not containing adults of *E. alaskanensis*. No rationale is given for synonymizing these species with *E. voxencollinus* which was described on the basis of non-diagnostic characters (Thor 1934) that could now apply to a number of species. Furthermore, since type material does not exist and so cannot be examined, I find the above synonymy doubtful.

Fig. 50. *Eupodes alaskanensis*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area, sagittal ♀ ;

(D) genital area, sagittal ♂ .

Scale intervals 10μm.

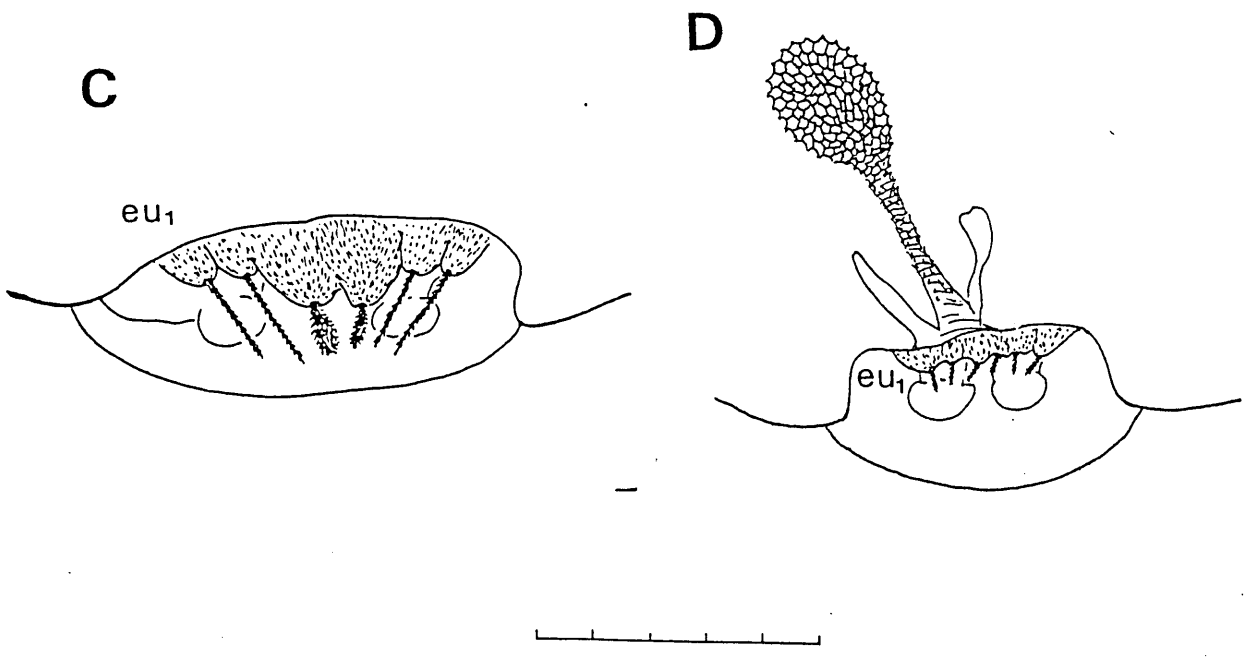
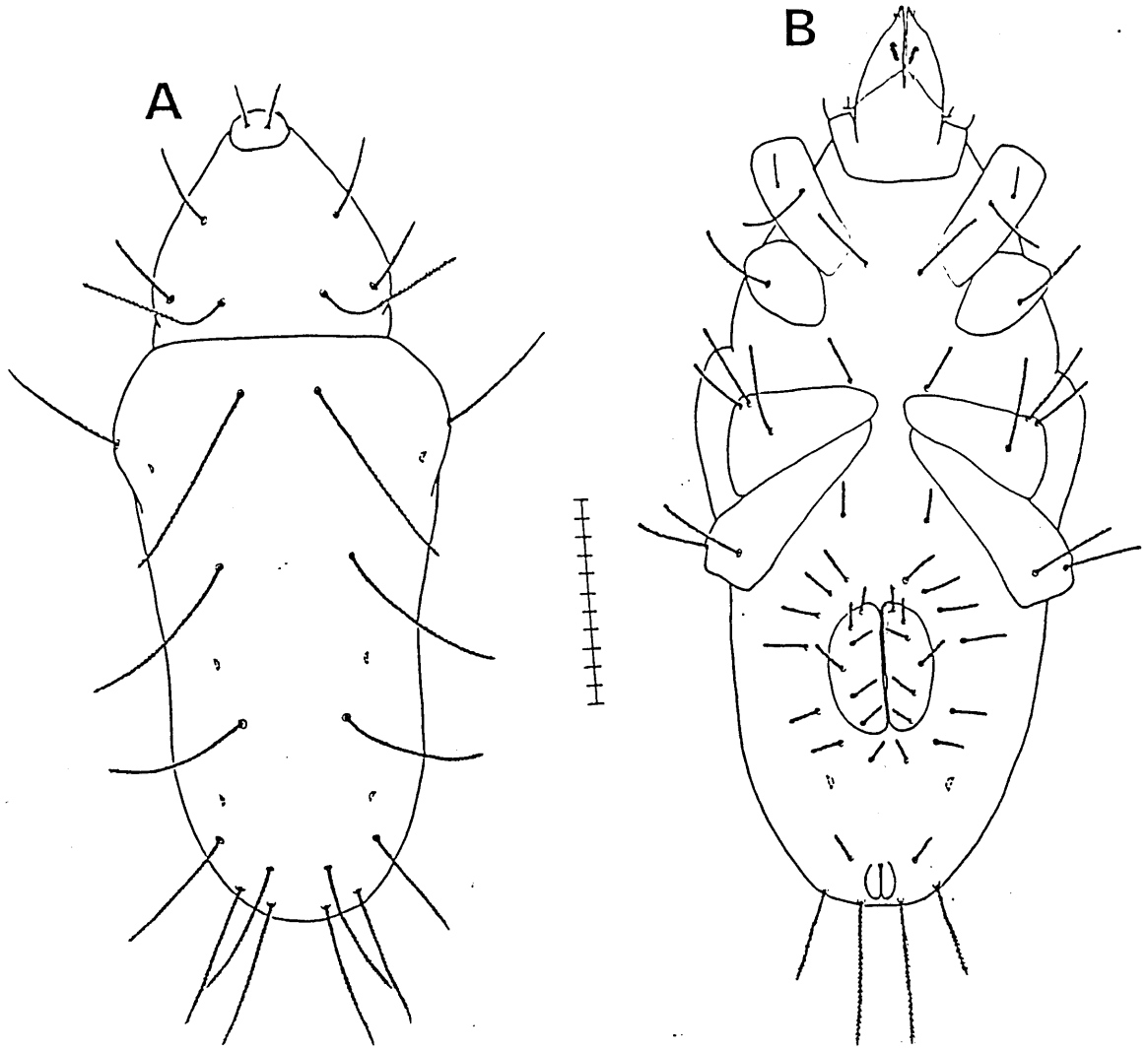
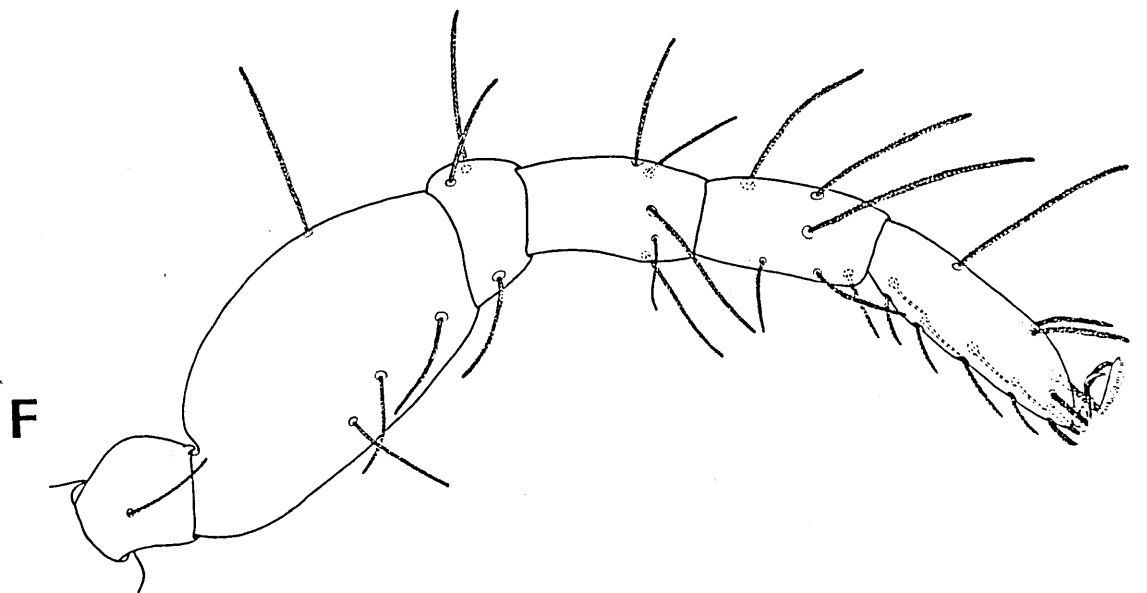
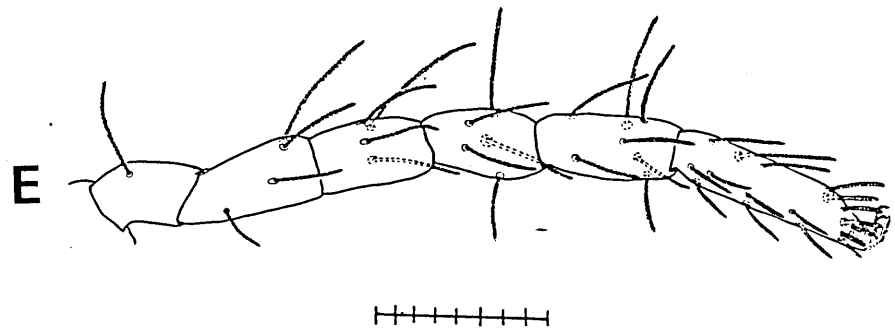
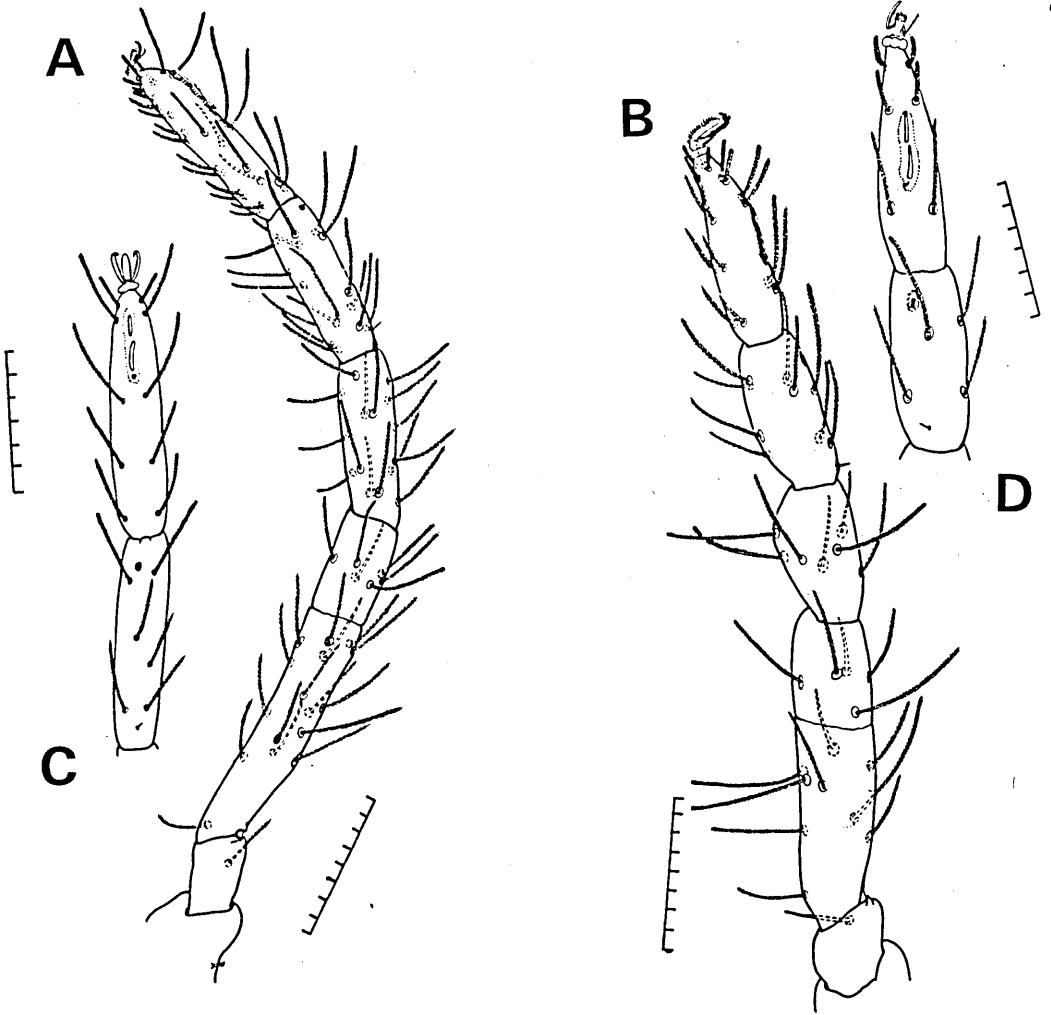


Fig. 51. *Eupodes alaskanensis*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Eupodes striatus n.sp.

Figs 52 & 53

DIAGNOSIS. *E. striatus* can be distinguished from other species of *Eupodes* by the presence of a conspicuous lateral band of striae and the terminal anus.

Body length 417 (410-421), width 199 (195-203).

GNATHOSOMA (Fig. 52B).

Subcapitulum: (*sbc*₁) 8 long, ca. half length of subapical (*sbc*₂).

Palp: typical for genus.

Chelicera: total length 89 (86-92) long; *cha* 11.

IDIOSOMA - DORSUM (Fig. 52A)

Setae: long, reaching the base of the following seta, lengths (*iv*) 25 (23-28), (*ev*) 53 (50-55), (*T*) 69 (65-73), (*sc*) 54 (51-57), (*c*₁) 66 (62-70), (*c*₂) 72 (67-76), (*d*₁) and (*d*₁) subequal ca. 64, (*f*₁) 69 (66-70), (*f*₂) 59 (57-63), (*h*₁) 72 (69-74), (*h*₂) 53 (49-56).

IDIOSOMA - VENTER (Fig. 52B,C)

Podosoma: (*a*) and (*b*) setae spatulate, remainder rounded; lengths (*1a* & *b*) subequal, ca. 30, (*1c*) 18, (*2b*) 38, (*3a*) 22, (*3b-c*) 31, (*4a*) 22, just over half length of (*4b* & *c*).

Genital area: eugenital setae rather long - (*eu*_{1,2,5,5}), slender tapering ca. 33 long, (*eu*_{3 & 4}) clavate, 21 long; genital setae subequal ca. 18 long; seven pairs of aggenitals, gradually decrease in length posteriorly from ca. 19 to 14.

Anal region: anus terminal, visible in dorsal view; (*ps*₁) 56 long, (*ps*₂) 44, (*ps*₃) 22.

LEGS (Fig. 53).

I just longer than body, II and III respectively just under and just below two-thirds, IV just below body length.

Setae: generally long; formulae I 1-20(15+5)-14-17-26,

II 1-14(9+5)-7-9-16, III 1-7(3+4)-5-5-14, IV 1-7(4+3)-5-6-13.

Solenidia & famuli: typical for genus; tibia I lacks distal rhagidial organ.

MALE. Unknown.

ETYMOLOGY. The specific name refers to the distinctive lateral ornamentation.

DISTRIBUTION. England, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, ENGLAND, Essex, Colne Point, Nature Reserve, approx. 500m south of North Mud Flats and 30m inland from North Horse Wash inlet, along *Sueda* path, from 3cm deep layer of soil under sea purslane (*Halimione portulacoides*), 12.v.1981 [BMNH, reg. no. 1987.3.23.61. Paratype 9♀♀, same data as holotype [BMNH, reg. nos 1987.3.23.7-151.

OTHER BRITISH RECORDS. ENGLAND, Kent, Canterbury Nature Reserve, grassy bank by power substation, from *Deschampsia/Agrostis* plus 2cm of underlying clay soil, 17.iii.1981; Cambridgeshire, Woodwalton Fen, Compartment 36, ground cover of common comfrey, from aerial parts of plant plus 2cm of wet underlying soil, 30.vi.1981; Wiltshire, Savernake Forest, approx. 1km south along South Path, from beech litter, 17.ix.1981. WALES, Capel Bangor, from top 3cm of litter under hawthorn hedge, 26.ii.1981.

Fig. 52. *Eupodes striatus* n.sp.:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital region ♀, sagittal.

Scale intervals 10µm.

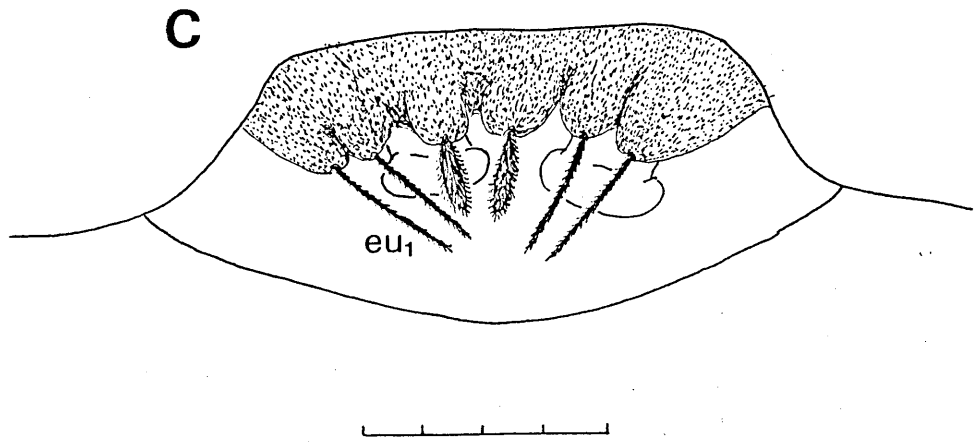
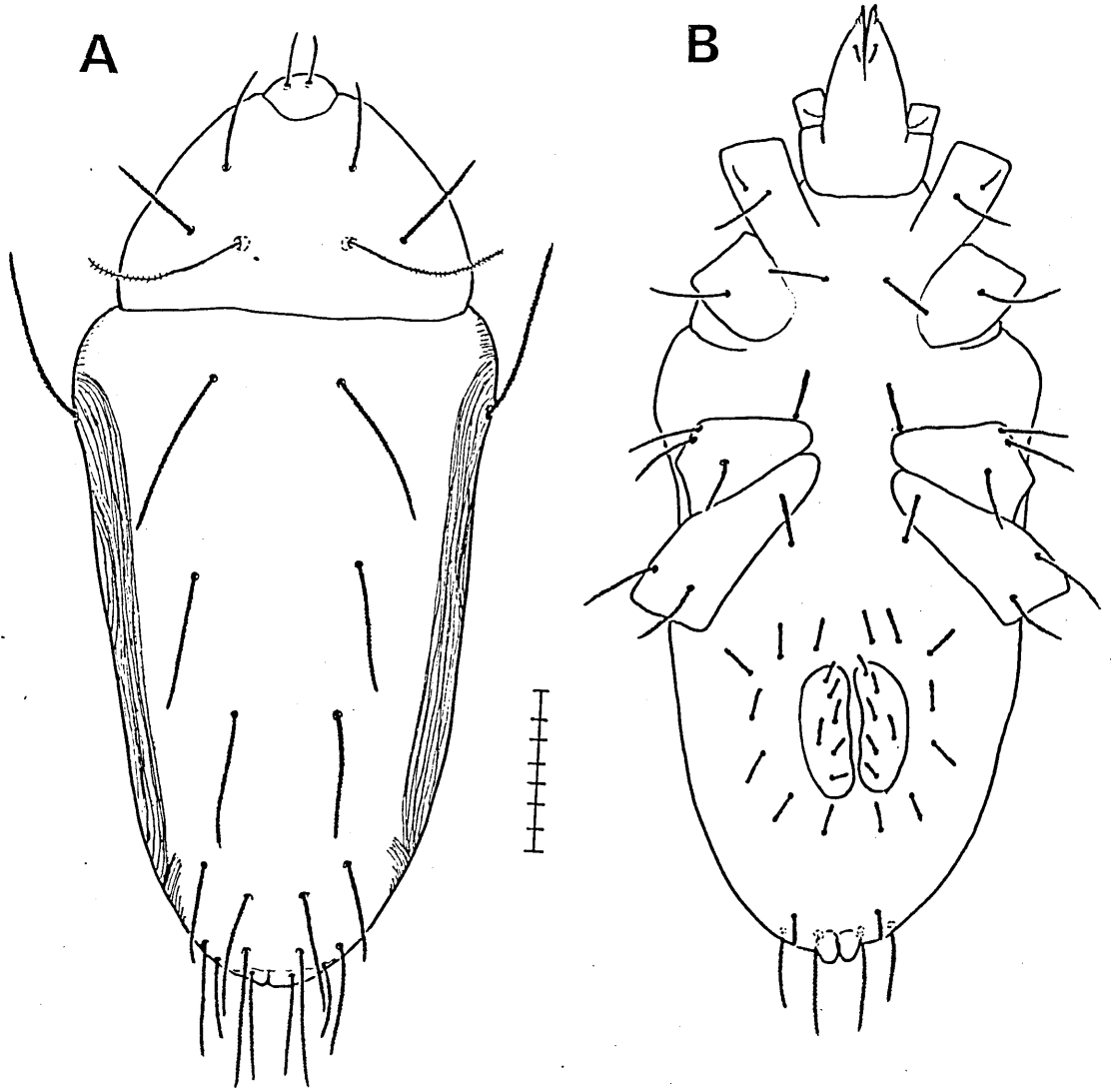
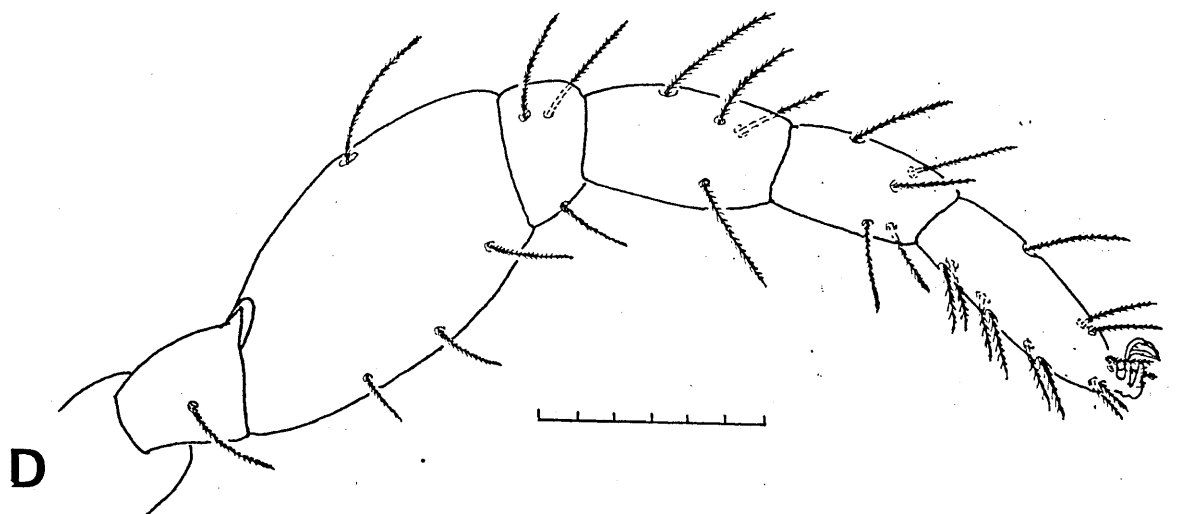
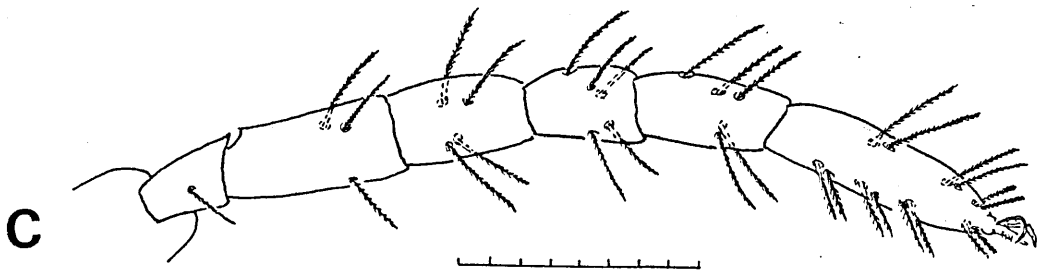
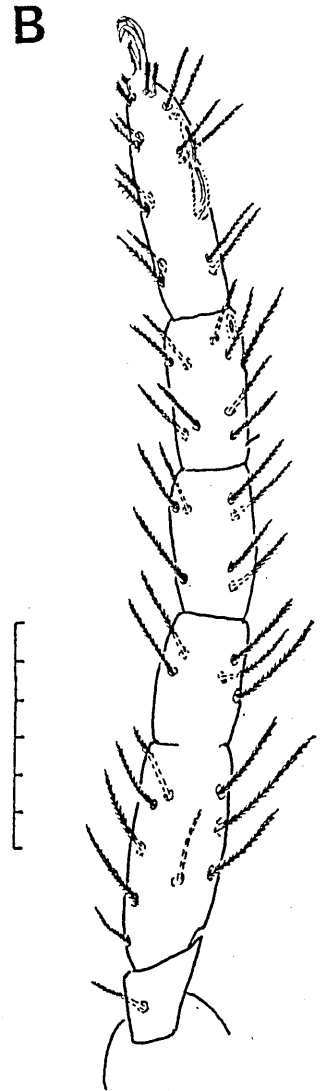
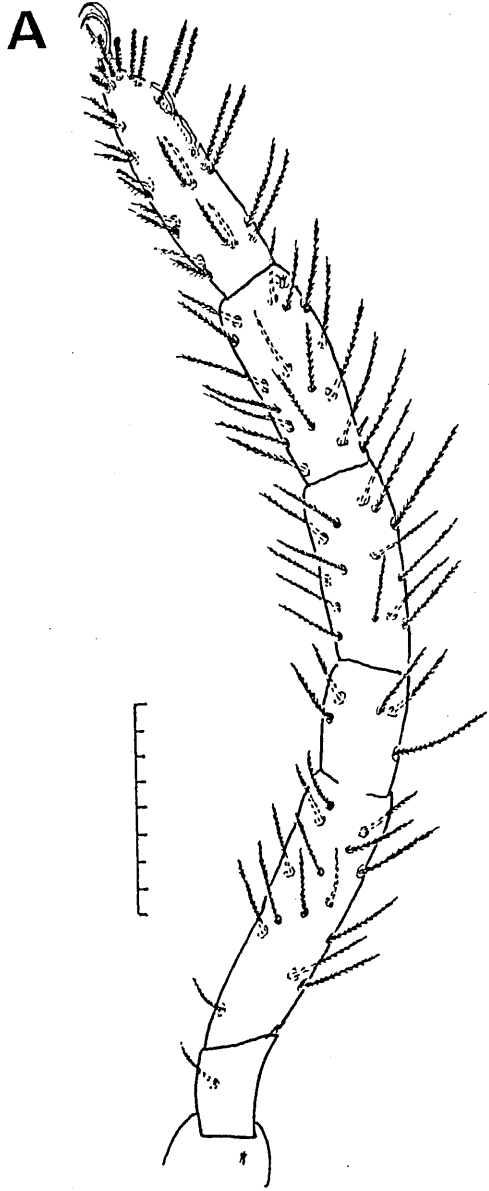


Fig. 53. *Eupodes striatus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) leg III, anterolateral;
- (D) leg IV, anterolateral.

Scale intervals 10 μ m.



Eupodes truncatus n.sp.

Figs 54 & 55

DIAGNOSIS. This species can be distinguished from other members of *Eupodes* by the short idiosomal setae, which do not reach the base of the seta posteriorly, the relatively indistinct sejugal furrow and by the leg chaetotaxy.

Body length 347 (323-363), width 153 (139-170).

GNATHOSOMA (Fig. 54B)

Subcapitulum: (sbc_2) 11 long approximately third longer than (sbc_1) and inserted ca. midway between (sbc_1) and anterior limit of subcapitulum.

Palp: typical for genus.

Chelicera: total length 76 (73-79); *cha* smooth, almost half length of fixed digit.

IDIOSOMA - DORSUM (Fig. 54A)

Eye-spots: observed in some specimens as dark, roughly circular, granular areas.

Setae: lengths - (*iv*) 18 (15-20), (*ev*) 25 (22-29), (*T*) 55 (51-58), (*sc*) 32 (30-35), (*c₁*) 34 (28-37), (*c₂*) 43 (41-46), (*d₁*) 36 (34-40), (*e₁*) 40 (38-44), (*f₁*) 43 (40-48), (*f₂*) 35 (31-77), (*h₁*) 45 (42-49), (*h₂*) 38 (34-41).

IDIOSOMA - VENTER (Fig. 54B,D)

Podosoma: *1a* 17 (15-20), *1b* at 20 (18-23) long approximately twice length (*1c*); *2a* 25 (21-27), (*3a*) and (*4a*) respectively 15 (13-18) and 13 (11-16), approximately half to two-thirds length of distal setae.

Genital area: ($eu_{1,2,5,6}$) approximately 17 long, slender and tapering, (eu_3 & 4) half as long and clavate, (eu_3) particularly so; genital setae subequal ca. 12 long; aggenital setae decrease in length posteriorly from ca. 17 to 13.

Anal region: (ps_1) and (ps_2) respectively 40 (35-44) and 23 (20-27) long, (ps_3) 17 (14-19).

LEGS (Fig. 55)

I approximately body length, II two-thirds times, III slightly shorter than II, IV just under body length.

Setae: formulae I 1-19(13+6)-14-11-20, II 1-12(7+5)-7-8-15, III 1-7(3+4)-5-6-13, IV 1-7(4+3)-5-6-12.

Solenidia & famuli: typical for genus; tibia I lacks distal rhagidial organ.

MALE. (Fig. 54C) (2 specimens examined). Sperm sac subclavate, unornamented.

ETYMOLOGY. The specific name refers to the rather shortened form of the idiodorsal setae.

DISTRIBUTION. Eire, England, Scotland, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, ENGLAND, Wiltshire, Savernake Forest, birch copse in east part, with patchy understorey brambles, from moss round base of birch, 17.ix.1981 [BMNH, reg.no. 1987.3.23.271]. Paratypes 9 ♀♀, same data as holotype [BMNH, reg.nos 1987.3.23.28-36], 2 ♂♂, same data as holotype [BMNH, reg.nos 1987.3.23.37-38].

OTHER BRITISH RECORDS. EIRE, Galway, Ryehill, Monivea, 22 miles NE of Galway, beech copse, from hollow of beech tree, 20.viii.1981 (K. P. Martyn). ENGLAND, Kent, Folkestone, The Warrens, grass covered limestone slope, from 12cm of aerial parts of rosebay willowherb and grass plus underlying 1cm of soil, 17.iii.1981. SCOTLAND, Fife, Abernethy Forest, from blueberry and moss amongst *Calluna* at edge of forest, 18.ix.1982. WALES, Dyfed, Tregaron, Cors Tregaron, raised path at edge of bog, by willow swamp, from mat of mixed moss by path, 24.ii.1981.

REMARKS. Short idiodorsal setae are also present in *E. wisei* (Womersley & Strandtmann 1963), but this species differs from *E. truncatus* by possessing only five pairs of aggenital setae and a rhagidial organ associated with the famulus of tibia I.

Fig. 54. *Eupodes truncatus* n.sp.:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area σ^7 , sagittal;

(D) genital area ρ , sagittal.

Scale intervals 10 μ m.

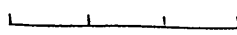
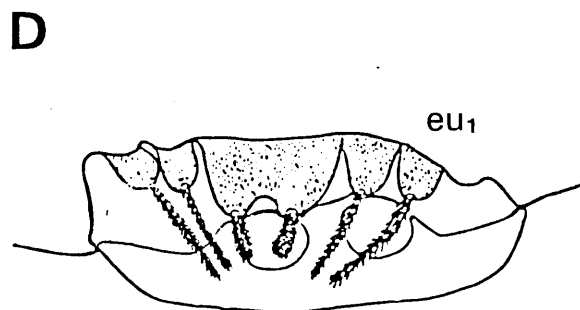
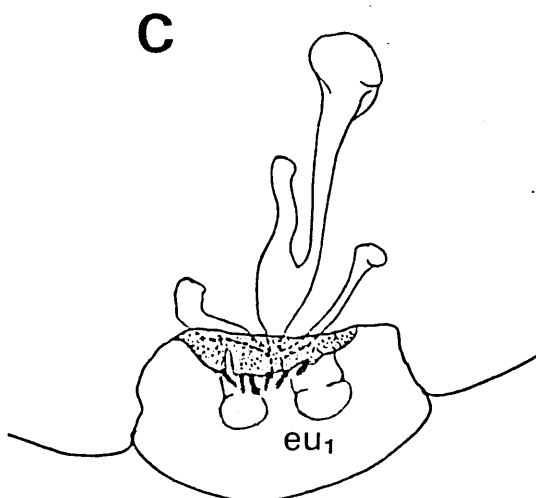
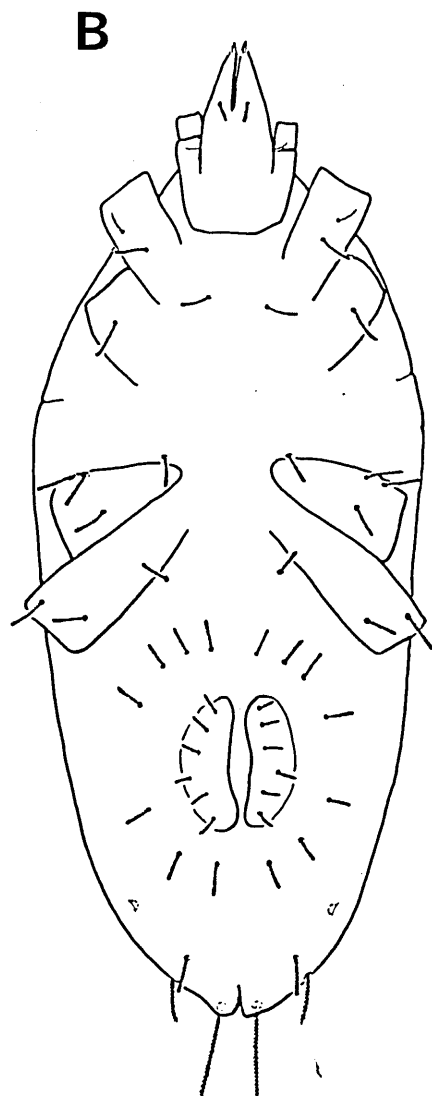
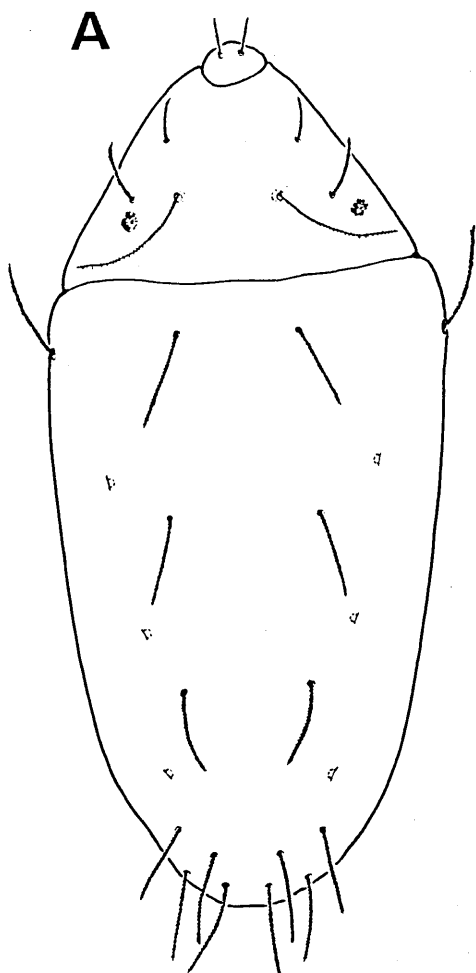
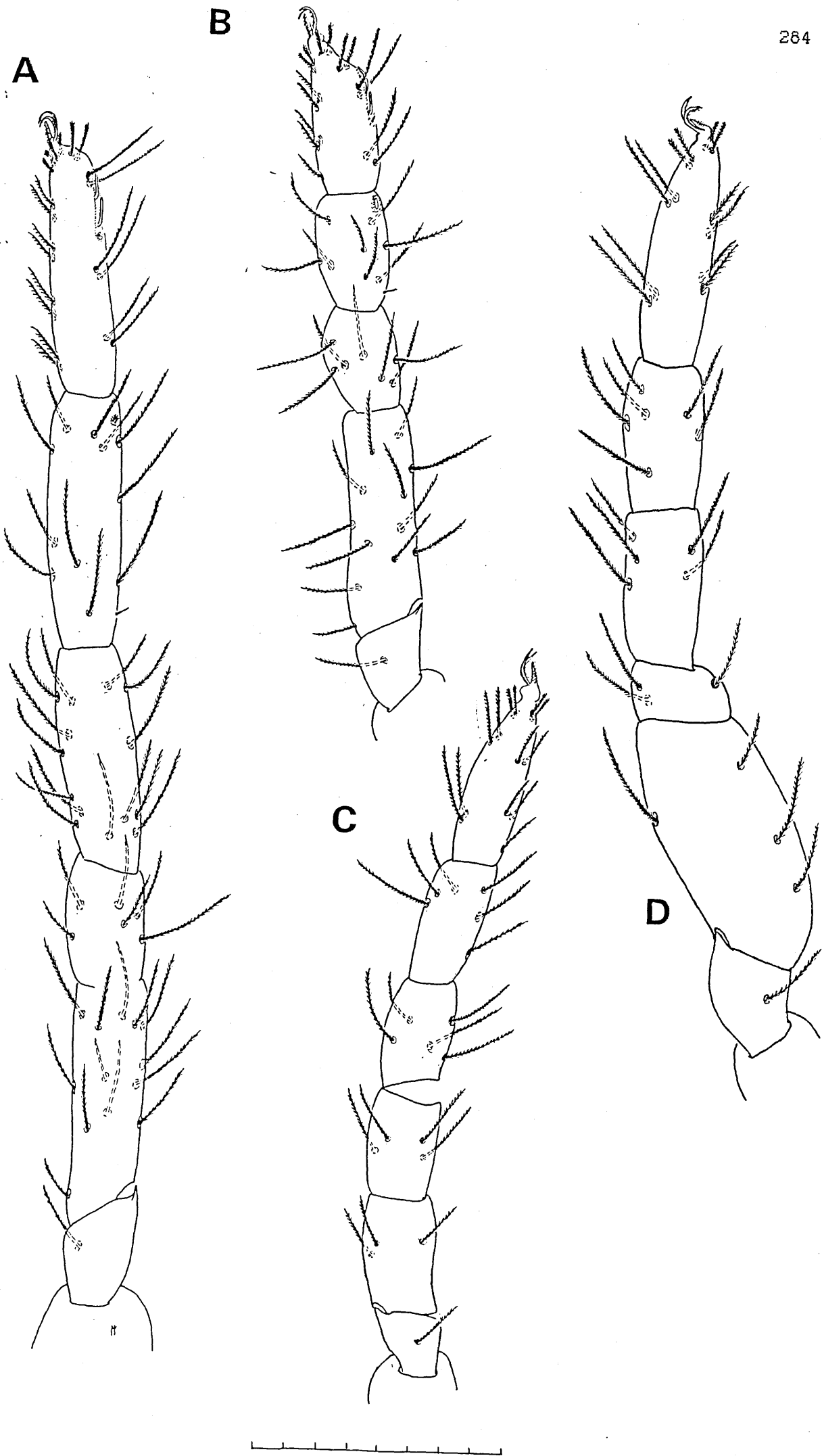


Fig. 55. *Eupodes truncatus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) leg III, anterolateral;
- (D) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.1.2 Genus *Alloepodes* n.gen.

Protereunetes Berlese, 1923: 245 [in part]. Thor & Willmann, 1941: 52 [in part]. Strandtmann, 1971: 82.

Eupodes: Strandtmann, 1970: 89 [in part].

DIAGNOSIS. Differs from other eupodid genera by possessing respectively four and three setae on coxae III and IV and three rhagidial organs on tarsus II.

DEFINITION.

Small (270-330).

Integument: weakly striate-papillate, prodorsal shield and appendages papillate.

GNATHOSOMA

Subcapitulum: ratio length to width 1:0.6; (*sbc*₁) approximately two-thirds length of (*sbc*₂), latter inserted approximately midway between (*sbc*₁) and anterior limit of subcapitulum.

Palp with ovoid tibiotarsus, length approximately twice widest part; supracoxal seta papillate.

Chelicera: chela account for approximately one-fifth of total length; fixed digit terminates in shallow fork; movable digit robust in proximal half, tapers suddenly to slender, recurved point; *cha* apparently smooth.

IDIOSOMA - DORSUM

Sejugal furrow clearly subdivides body into roughly triangular prodorsum and opisthosoma gradually tapering to rounded posterior.

Naso clearly delimited lobe but without separating dorsal suture.

Setae: (*iv*) located on epivertex; (*ev*) just lateral and anterior to (*D*); (*sc*) inserted lateral to (*D*); setae of *c* and *f* row in line; (*D*) spiculated, markedly so in distal two-thirds, relatively short extending just past sejugal furrow; remaining setae spinose, short.

Lyrifissures: round.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-3; setae simple, densely spinose, tapering.

Genital area with six pairs simple, tapering, densely spinose eugenital setae; six pairs simple, spinose genital setae in single file; four or five pairs simple, spinose aggenital setae.

Anal region: anus subterminal; three pairs simple, spinose pseudanal setae; (*ih*) anterior and just lateral to (*ps₃*).

LEGS

Slender, all shorter than body, I approximately three-quarters body length.

Setae: spinose, mostly shorter than segments.

Solenidia & famuli: rhagidial organs T-shaped; respectively two and three rhagidial organs on tarsus I and II; famuli in same pit and just posterolateral to base of proximal organ; two rhagidial organs, one proximally and one distally, on tibia I and II; one solenidion on genua I to III; rhagidial organ often present on tibia IV.

Apotela: all of similar form.

MALE. Sperm sac clavate, unornamented, though can have granular appearance.

TYPE SPECIES. *Alloeupodes interruptus* n.sp.

ETYMOLOGY. The generic name is derived from the greek word 'allos', meaning another kind of, and pertains to the establishment of another genus to accommodate species that have recently been included in the genus *Eupodes*.

REMARKS. *Alloepodes* includes species which previously would have been classified in the genus *Protereunetes*. The latter was declared invalid by Fain (1964) when he found the type species, *P. agilis*, to be an ereynetid.

The following species are also classified in the genus *Alloepodes*:

A. crozetensis (Strandtmann and Davies 1972) **n.comb.**

A. exiguous (Booth, Edwards & Usher 1985) **n.comb.**

A. minutus (Strandtmann 1967) **n.comb.**

A. paulinae (Gless 1972) **n.comb.**

Alloeupodes interruptus n.sp.

Figs 14b, 18f, 23g, 56 & 57

DIAGNOSIS. *A. interruptus* can be distinguished by the isolated position of the last pair of genital setae (g_5) and by the unequal size of the tarsal rhagidial organs.

Body length 280 (261-289), width 129 (125-136).

GNATHOSOMA (Figs 23g, 56C,D,E)

Subcapitulum: (sbc_1) ca. 5 long; (sbc_2) 7.

Palp: typical for genus.

Chelicera: total length 54 (51-56); cha 3 long, located in slight depression.

IDIOSOMA - DORSUM (Figs 14b, 56A)

Eyes: present as semi-circular outline just lateral and anterior to (sc).

Setae: lengths (iv) 12, (ev) 19, (sc) 17, (T) 51, (c_2) 18, (c_1), (d_1), (e_1) subequal ca. 11, (f_1) 16, (f_2) 18, (h_1) 21, (h_2) 18.

VENTER - DORSUM (Figs 56B,G)

Podosoma: ($1a$) and ($1b$) subequal, ca. 14, ($1c$) half as long, ($2b$) 13, ($3a-d$) subequal ca. 11, ($4a-c$) subequal ca. 10.

Genital area: eugenital setae subequal, ca. 6 long; genital setae, (g_{1-5}) spread evenly along anterior half of shields, (g_5) inserted close to posterior limits, (g_1 & 2) simple, spinose, ca. 9 long, twice as long as slightly clavate spinose (g_{3-5}), (g_5) simple, spinose ca. 6 long; aggenital setae subequal, ca. 8 long.

Anal region: (ps_3) 10 long; (ps_1 & 2) respectively 13 and 15 long.

LEGS (Figs 18f, 57)

I just over, IV just below two-thirds body length, II and III approximately half body length; tarsus I appears slightly inflated.

Setae: trochanteral setae of I and II fine, apparently smooth; formulae I 1-12(7+5)-6-5-20, II 1-10(5+5)-4-5-13, III 1-8(4+4)-4-4-12, IV 1-6(3+3)-3-5-11.

Solenidia & famuli: proximal rhagidial organ of tarsus I enlarged, ca. three times size of distal; proximal organ of tibia I small, ovoid in circular pit; genu I with ovoid rhagidial organ dorsally just in proximal half of segment, in lateral view appears to be subcuticular and funnel-shaped; rhagidial organs of tarsus II subequal; solenidium of genua II and III semi-erect.

MALE. (Fig. 56F) (1 specimen examined). Sperm sac subclavate, unornamented; accessory gland weakly striated.

ETYMOLOGY. The specific name refers to the uneven distribution of the genital setae.

DISTRIBUTION. England, Scotland, Wales.

MATERIAL EXAMINED. Holotype ♀, ENGLAND, Suffolk, Hollesley Common, from rotting pine wood, 4.ii.1985 [BMNH, reg. no. 1987.3.23.16]. Paratypes 5 ♀♀, 1♂, same data as holotype, 4 ♀♀, Wiltshire, Savernake Forest, approximately 900m south of junction of main paths, oak copse edged by hawthorn, from litter and fermentation layers under oak, 17.ix.1981 [BMNH, reg. nos 1987.3.23.17-26].

OTHER BRITISH RECORDS. ENGLAND, Yorkshire, Wigglesworth, from moss at base of stone wall by ditch, 18.ii.1982; Cambridgeshire, Woodwalton Fen, Plot 85, rough pasture, from fresh molehill on path along, SW edge of compartment 79, 30.vi.1982. SCOTLAND, Strathclyde, western shore of Loch Lomond, from bracken litter in birch copse, 12.ix.1982. WALES, Dyfed, Capel Bangor, from litter under newly felled hawthorn hedge, 26.ii.1981.

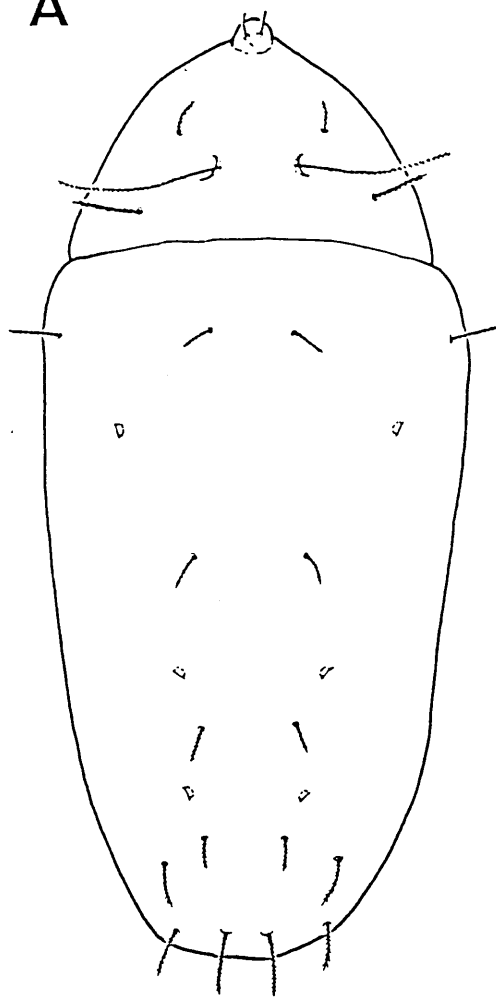
REMARKS. *A. interruptus* was found only from the above localities.

Fig. 56. *Alloepodes interuptus* n.sp.:

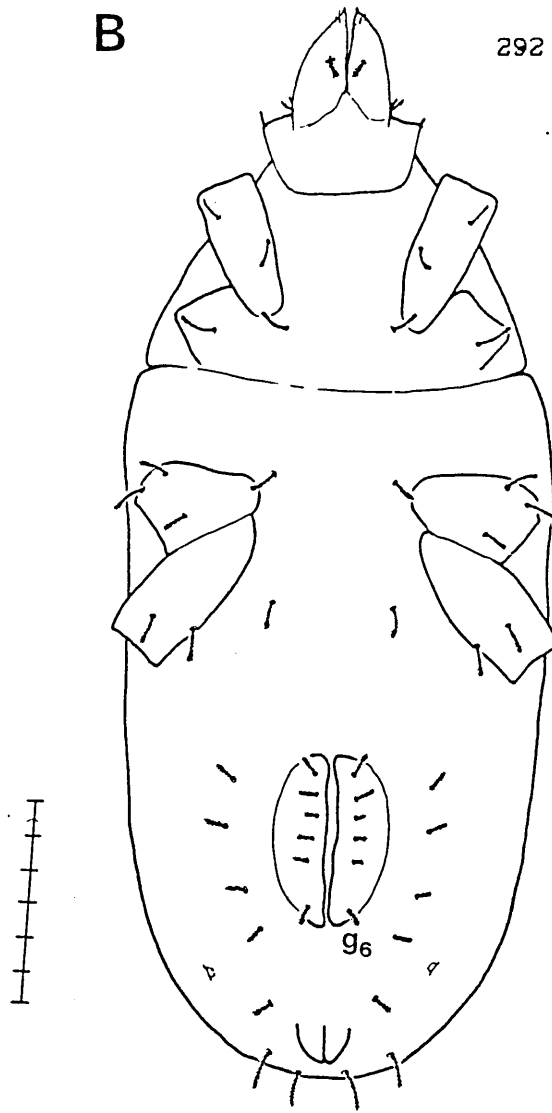
- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) chelicera, antiaxial;
- (E) palp, antiaxial;
- (F) genital area σ^7 , sagittal;
- (G) genital area φ , sagittal.

Scale intervals 10 μ m.

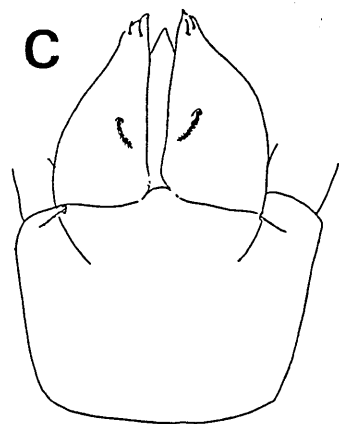
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B



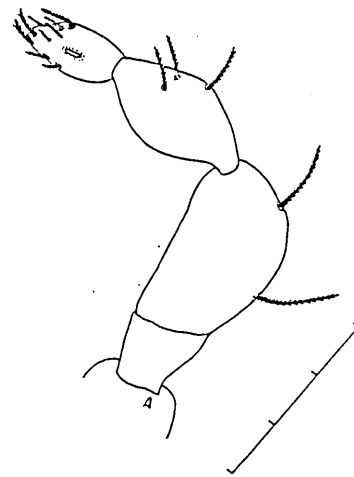
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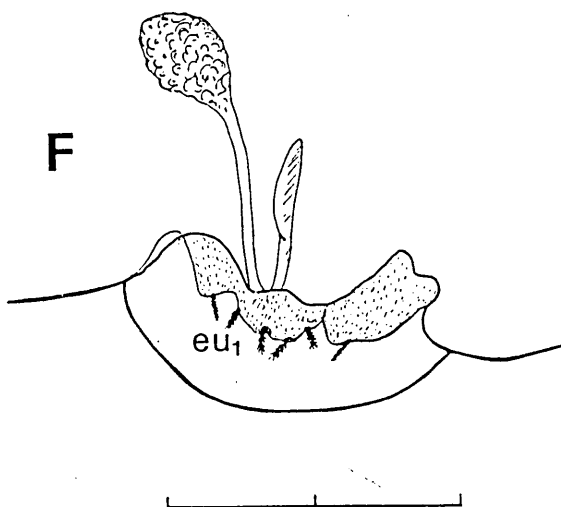
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E



F



G

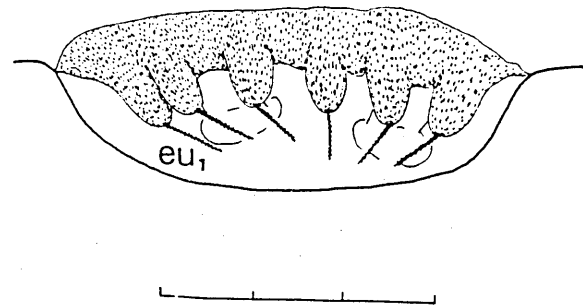
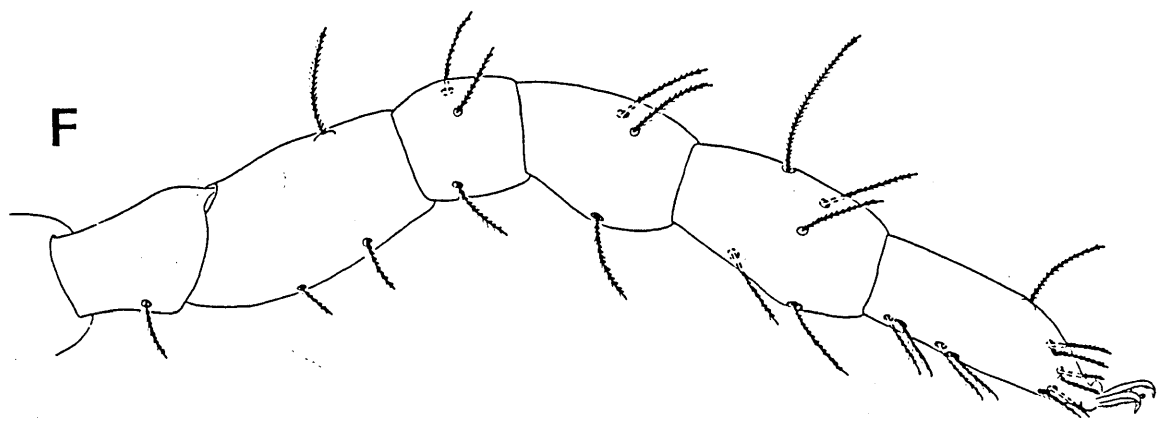
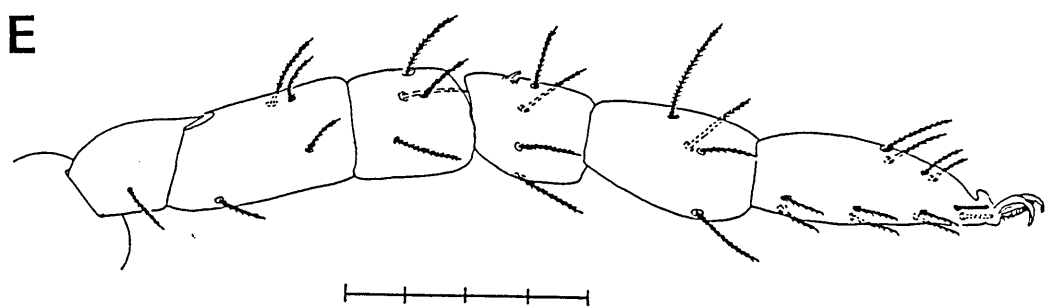
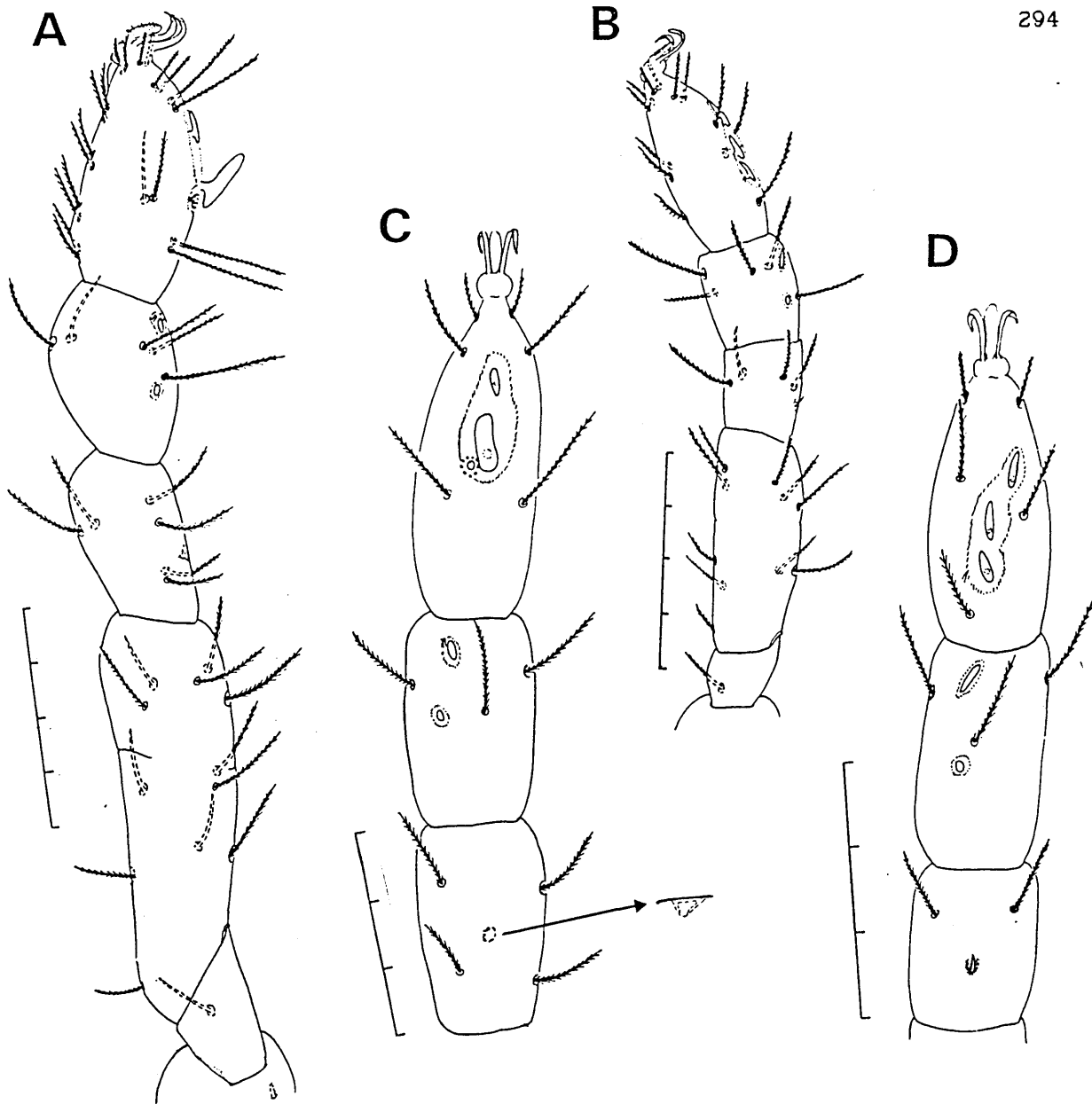


Fig. 57. *Allo eupodes interruptus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus, tibia & genu I, dorsal, with lateral detail of
rhagidial organ;
- (D) tarsus, tibia & genu II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.1.3 Genus *Anebaeupodes* n.gen.

DIAGNOSIS. Can be distinguished from other eupodid genera by the presence of only two setae on coxa IV.

DEFINITION.

Small (274-410), lightly sclerotized.

Integument of idiosoma weakly striate-spiculate, prodorsal shield and appendages papillate.

GNATHOSOMA

Subcapitulum: ratio length to width 1:0.5; (sbc_1) ca. half length of (sbc_2), latter located just under halfway between (sbc_1) and anterior limit.

Palp with long, slender tibiotarsus, ca. three times longer than widest part; supracoxal seta terminates in crown of spicules.

Chelicera with chela deflected ventrally, accounting for approximately one-fifth of total length; fixed digit terminates in shallow fork; movable digit robust in proximal half, slender in distal; *cha* smooth.

IDIOSOMA - DORSUM

Sejugal furrow clearly subdivides body into roughly triangular prodorsum and opisthosoma with shoulders narrowing slightly to broadly rounded posterior.

Naso: clear lobe, without dorsal delimiting suture.

Setae: (*iv*) inserted on naso; (*ev*) located approximately one fifth distance from (*T*) to anterior limit of prodorsum; (*sc*) just lateral to (*T*); respective setae of *c* and *f* row in line; (*T*) filiform, spiculated, markedly so in distal two-thirds inserted in markedly large bothridia;

remaining setae simple, spinose, short; base of (f_1) enlarged, bothridia-like, but seta normal.

Lyrifissures: round.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-2; setae spinose, blunt.

Genital area: six pairs tapering, densely spiculated eugenital setae, mounted on tubercles; six pairs genital, in single file, and aggenital setae, all spinose, blunt.

Anal region: anus subterminal; two pairs pseudanal setae; (ps_1) markedly longer than (ps_3).

LEGS

All shorter than body; all segments slender.

Setae: shorter than segments, spinose; formulae I 1-12(7+5)-7-8-18, II 1-10(5+5)-4-5-12; III 1-8(4+4)-4-5-11, IV 1-5(2+3)-4-4-11.

Solenidia & famuli: rhagidial organs L-shaped, respectively two and three on tarsi I and II, organs and famuli variously located; one distal rhagidial organ and a proximal erect spiniform solenidion on tibiae I and II, famulus of tibia I associated with rhagidial organ; genua I and II with erect spiniform solenidion.

Apotela: all of similar form.

MALE. With subclavate sperm sac, unornamented.

TYPE SPECIES. *Aneboeupodes minimus* n.sp.

ETYMOLOGY. The name is taken from the greek 'anebos', meaning young, and refers to the nymphal complement of coxal setae.

DISTRIBUTION. England, Scotland, Wales.

REMARKS. To date, the two species described from the British fauna are the only members of this genus.

Key to the British species of *Aneboeupodes*

1. Idiosoma less than 300 long; proximal rhagidial organ of tarsus I about two times length of distal; rhagidial organs of tarsus II slightly overlapping, short spiniform famulus located near base of proximal organ; solenidion of genu II located near distal margin of segment *A. minimus* n.sp.
2. Idiosoma over 400 long; rhagidial organs of tarsus I subequal; rhagidial organs of tarsus II in tandem, relatively longer famulus located at level of junction of two proximal organs; solenidion of genu II located approximately three-quarters distance along segment *A. magnus* n.sp.

Aneboeupodes minimus

Figs 58 & 59

DIAGNOSIS. Can be distinguished from *A. magnus* by its smaller size, by the proximal rhagidial organ of tarsus I being approximately two times the distal, the slightly overlapping rhagidial organs of tarsus II, the shorter famulus located near the base of the proximal organ and the more distal position of the erect solenidion of genu II.

Body length 261 (250-271), width 125 (119-129).

GNATHOSOMA (Figs 58C,D,E)

Subcapitulum: (*sbc*₁) ca. 4, (*sbc*₂) 10 long.

Palp: typical for genus.

Chelicera: total length 58 (56-61); *cha* 3 long.

IDIOSOMA - DORSUM (Fig. 58A)

Setae: lengths (*iv*) 7, (*ev*) 10, (*sc*) 12, (*T*) 45, (*c*₂) 20, (*c*₁), (*d*₁), (*e*₁) subequal ca. 14, (*f*₁) 30, (*f*₂) 20, (*h*₁) 17, (*h*₂) 18.

IDIOSOMA - VENTER (Fig. 58B,G)

Podosoma: setal lengths - (*1a*) and (*1b*) subequal, ca. 12, (*1c*) 7, (*2b*) 10, (*3a-d*) subequal ca. 11, (*4a-c*) subequal ca. 9.

Genital area: eugenital setae increase in length posteriorly from ca. 6 to 10; genital setae subequal, ca. 8 long; aggenital setae subequal, ca. 10.

Anal region: (*ps*₁) 13 long; (*ps*₂) 10.

LEGS (Fig. 59)

I just over, IV just below two-thirds body length, II and III approximately half body length.

Setae: formulae as for genus.

Solenidia & famuli: tarsus I with rhagidial organs in tandem in confluent pits, proximal two times length of distal, famulus in separate pit posterolaterally near base of ω_1 ; erect solenidion of genua I near distal margin; tarsus II with slightly overlapping rhagidial organs in confluent pits, famulus in separate pit posterolaterally just beyond base of ω_1 ; genu II with erect solenidion near distal margin of segment.

MALE. (Fig. 58F) (1 specimen examined). Sperm sac subclavate, unornamented.

ETYMOLOGY. The specific name refers to the small size of this species.

DISTRIBUTION. England.

MATERIAL EXAMINED. Holotype ♀, ENGLAND, Surrey, Chobham Common, from litter and soil under gorse, 19.v.1982 [BMNH, reg. no. 1987.3.24.14]. Paratypes 5 ♀♀; Oxfordshire, Wytham Wood, Holly Hill, from sycamore litter, approximately 4cm deep, 23.11.1982; 3 ♀♀, 1♂, same locality, from hawthorn litter, 23.xi.1982 [BMNH, reg. nos 1987.3.24.15-23].

OTHER BRITISH RECORDS. ENGLAND, Leicestershire, 12km S of Hinckley, area of oak woodland, from fermentation layer under oak, 19.ii.1982; Northumberland, Bolam Lake, from moss mat covering rocks by lake, 22.ii.1982; Tyne & Wear, Tynemouth, below Castle ruins, from tuft of grass and underlying soil approximately 1.5m from base of cliff, 24.ii.1982.

Fig. 58. *Aneboeupodes minimus* n.sp.:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial;
- (F) genital area σ^7 , sagittal;
- (G) genital area φ , sagittal.

Scale intervals 10 μ m.

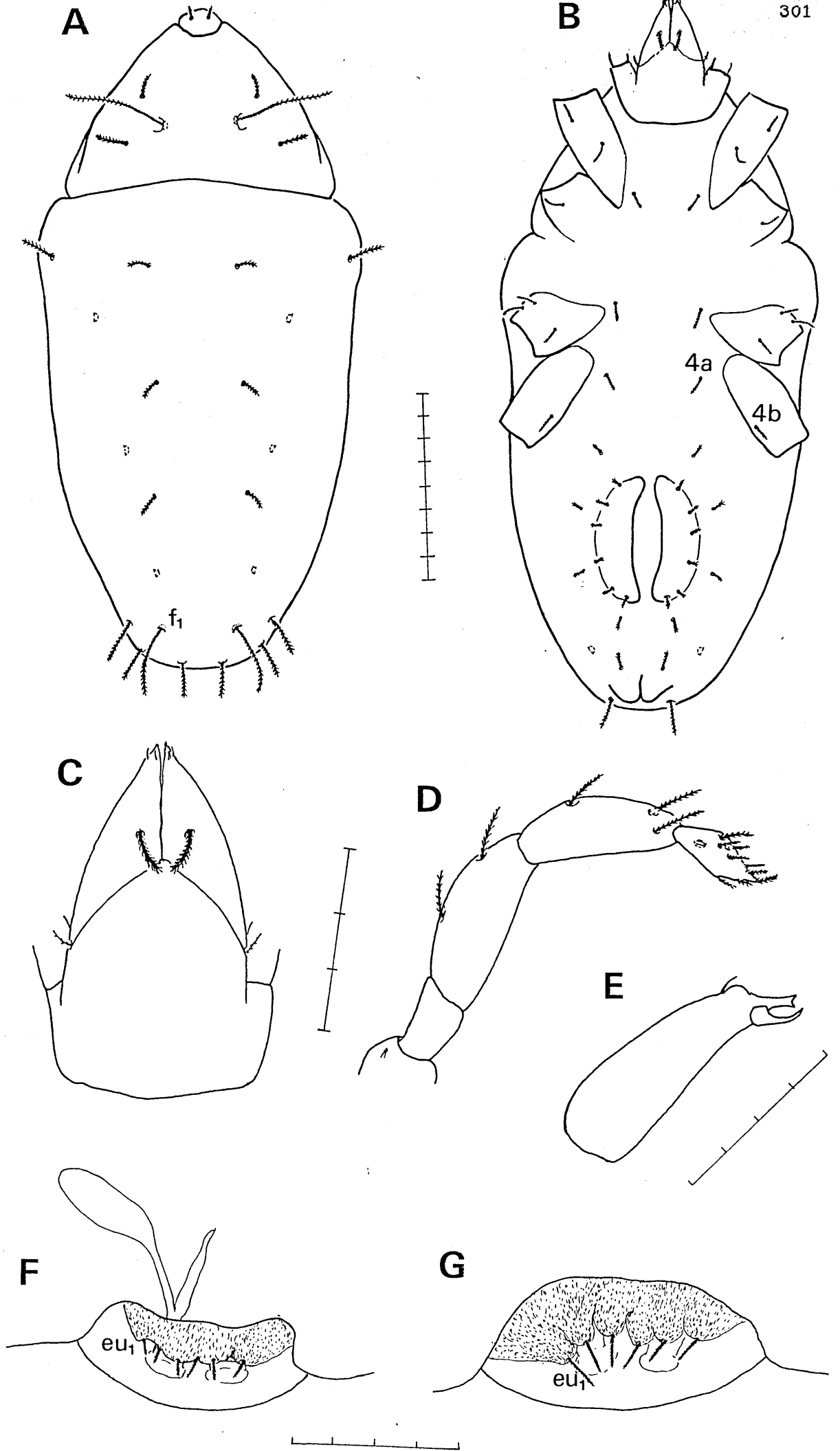
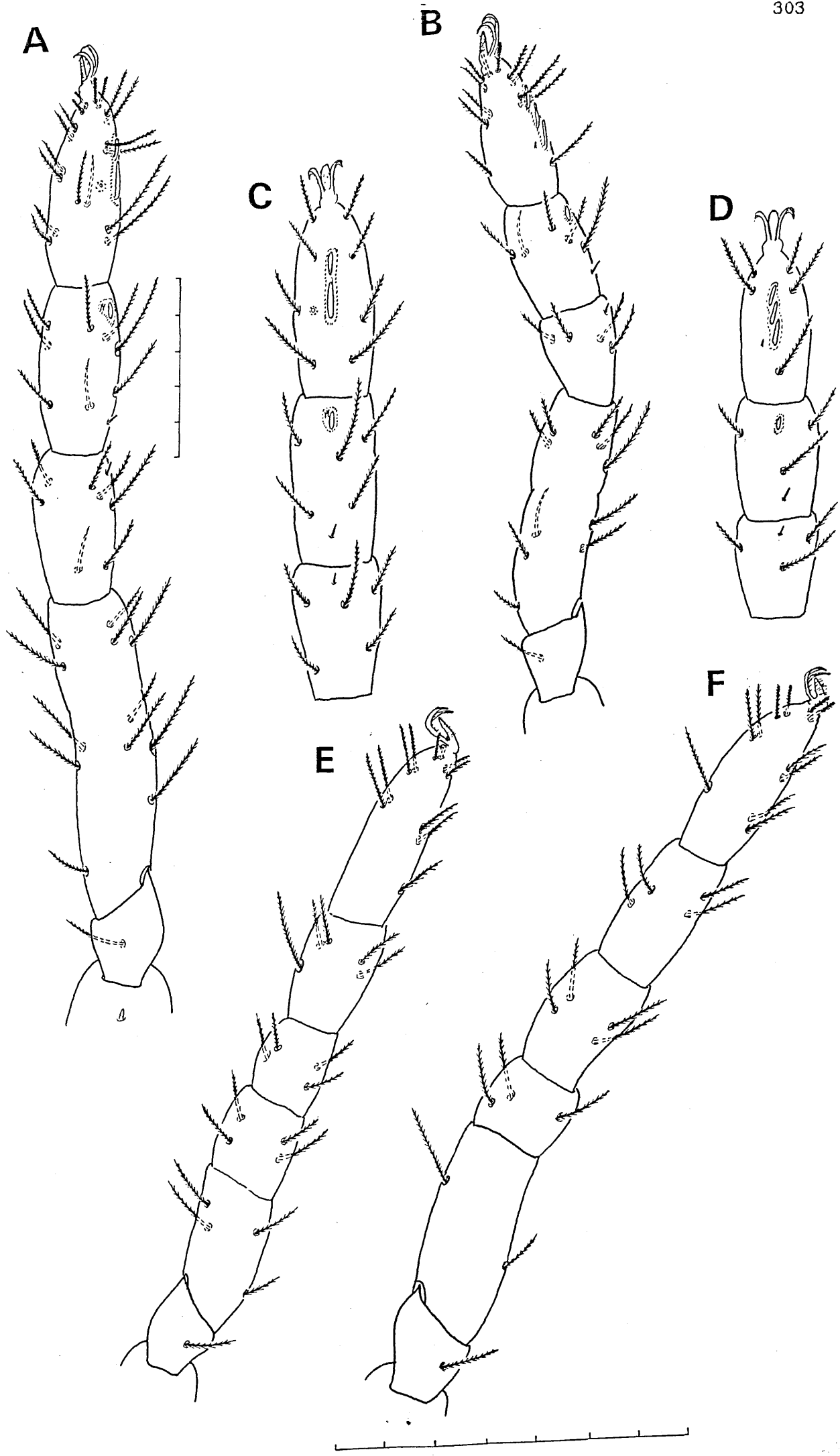


Fig. 59. *Aneboeupodes minimus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus, tibia & genu I, dorsal;
- (D) tarsus, tibia & genu II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Aneboeupodes magnus n.sp.

Figs 60 & 61

DIAGNOSIS. Differs from *A. minimus* by its larger size, the subequal rhagidial organs of tarsus I, the serial arrangement of the rhagidial organs of tarsus II, the more anterior position and larger size of famulus II and the relatively distal position of the erect solenidion on genu II.

Body length 410 (401-419), width 180 (172-192).

GNATHOSOMA (Fig. 60B)

Subcapitulum: (*sbc*₁) 6, (*sbc*₂), ca. 13 long.

Chelicera: total length ca. 79 (76-81); *cha* 7 long.

Palp: typical for genus.

IDIOSOMA - DORSUM (Fig. 60A)

Setae: (*iv*) 10, (*ev*) 23, (*T*) 64, (*sc*) 30, (*c*₁) 25, (*c*₂) 37, (*d*₁)

(*e*₁) subequal ca. 27, (*f*₁) 42, (*f*₂) 25, (*h*₁) 33, (*h*₂) 27.

IDIOSOMA - VENTER (Figs 60B,C)

Podosoma: *1c*, at 11 long, approximately half length of *1b* & *c*, *2b* 19, *3a-d* subequal, ca. 16 long, *4a* 16, just over three-quarters length of *4b*.

Genital area: (*eu*₃) finer than and slightly lateral to others; genital setae decrease in length posteriorly from 14 to 11; (*ag*₁ & ₂) 16 long, remainder subequal, ca. 11.

Anal region: (*ps*₁) 32, just over three times length of (*ps*₃).

LEGS (Fig. 61)

I approximately two-thirds, II and III slightly over half and IV just under two-thirds body length.

Setae: formulae as for genus.

Solenidia & famuli: tarsal rhagidial organs in tandem and confluent pits; those of I subequal, famulus located separately approximately halfway along proximal rhagidial organ; those of II decrease in size slightly distally, famulus relatively long, located separately at level of junction of two proximal rhagidial organs; rhagidial organ of tibia II at an oblique angle; genua I and II with an erect solenidion dorsally respectively near distal margin and three-quarters way along segment.

MALE. Unknown.

ETYMOLOGY. The specific name refers to the relatively large size of this member of the genus.

DISTRIBUTION. Scotland, Wales.

MATERIAL EXAMINED. Holotype ♀, WALES, Dyfed, Borth, Ynyslas Nature Reserve, Beach debris around HWM, mostly seaweeds with some oak leaves, 25.ii.1981 (BMNH, reg.no. 1987.3.24.24). Paratypes 5 ♀♀, same data as holotype; 4 ♀♀, same locality as holotype, from clump of *Juncus maritimus* approximately 10m below top of saltmarsh, 25.ii.1981 (BMNH, reg. nos 1987.3.23.33).

OTHER BRITISH RECORDS. SCOTLAND, Shetland Islands, Lerwick, 6km SW of Gulberswick, from *Sphagnum*, 5.vii.1963 (M. E. Bacchus).

REMARKS. Although *A. magnus* was found only from the above localities, these limited records suggest it might be a submarine species.

Fig. 60. *Aneboeupodes magnus* n.sp.:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area φ , sagittal.

Scale intervals 10 μ m.

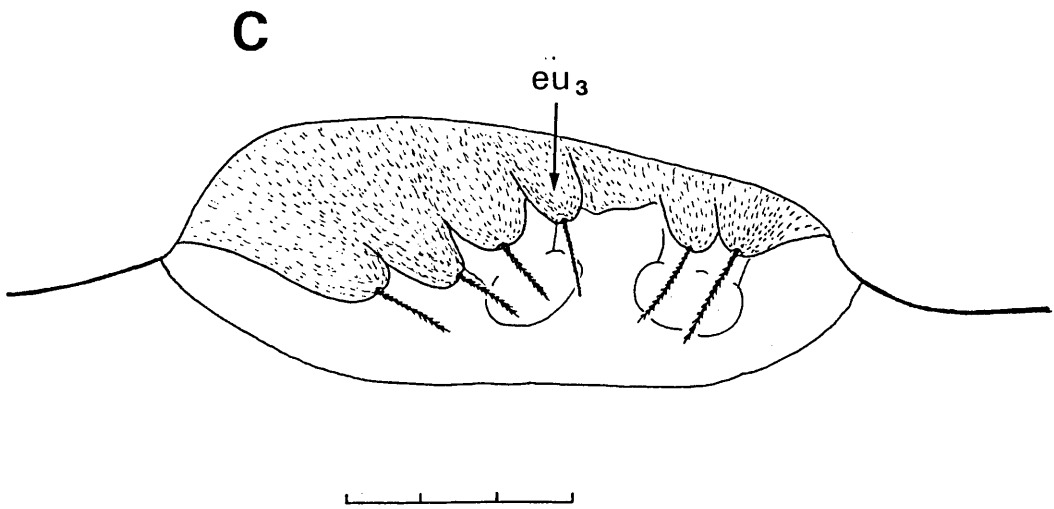
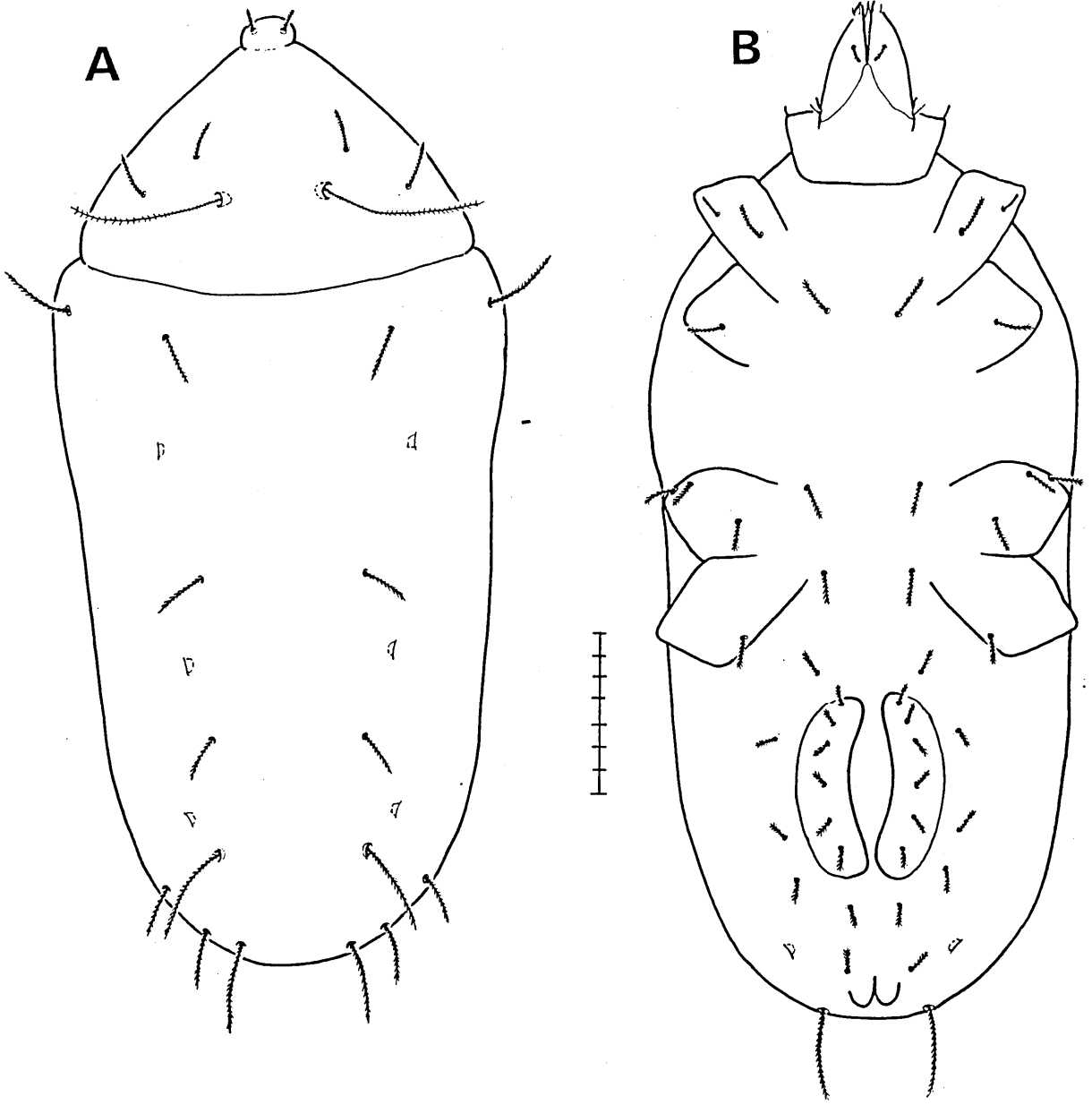
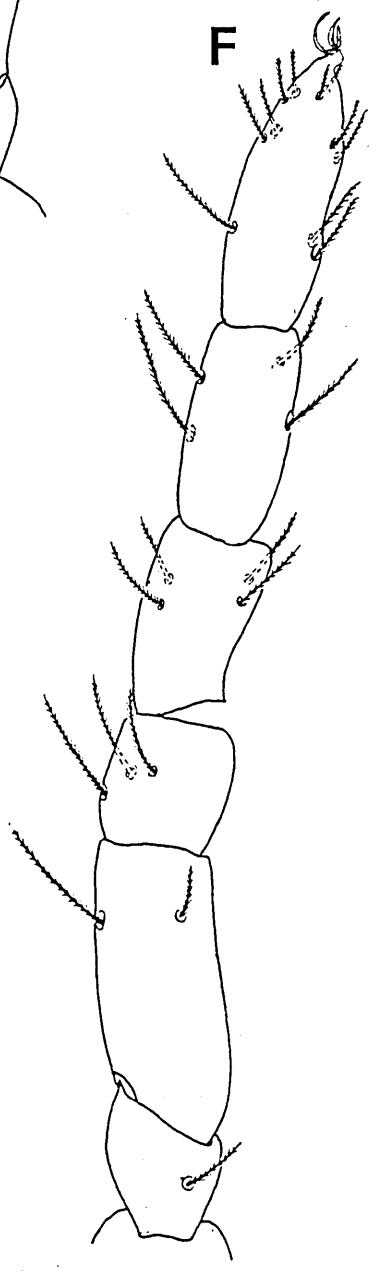
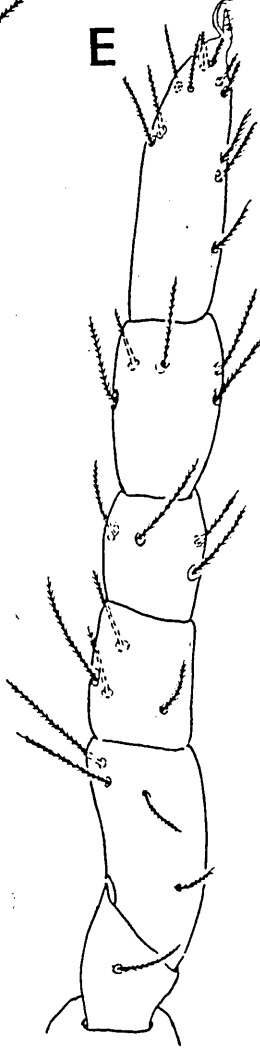
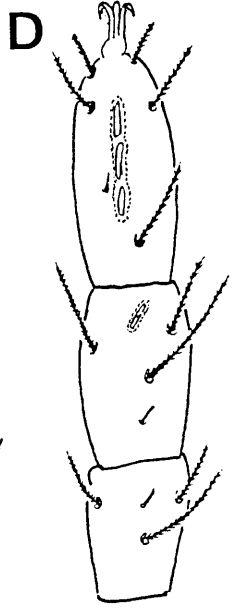
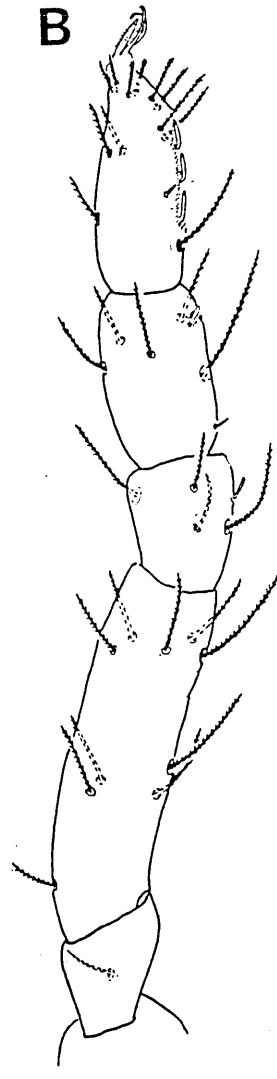
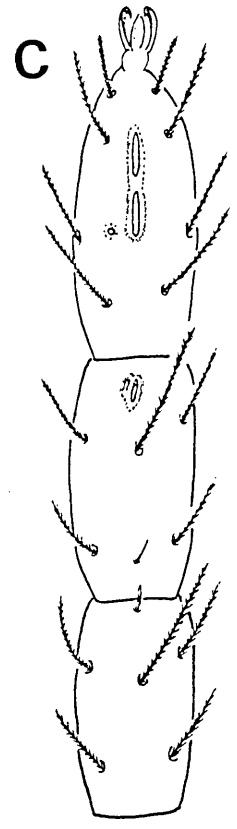
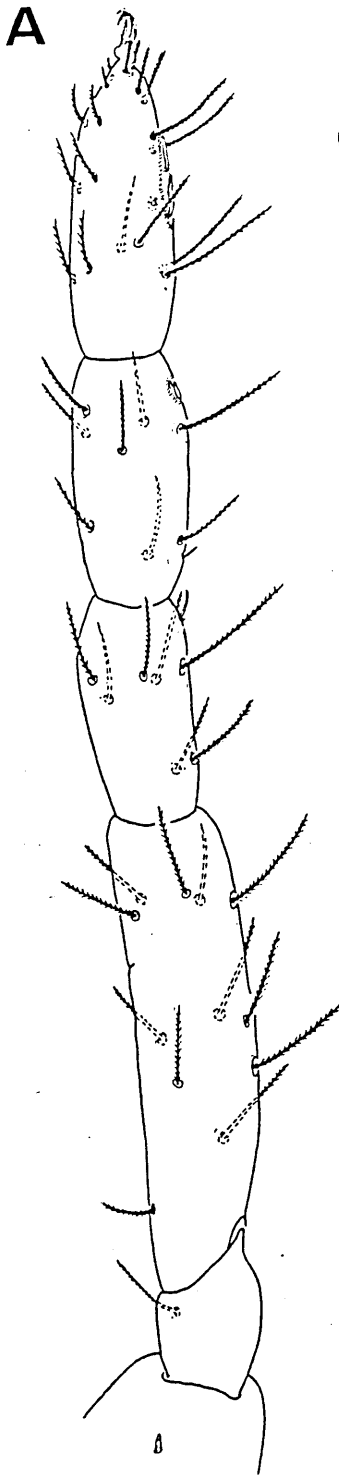


Fig. 61. *Aneboeupodes magnus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus, tibia & genu I, dorsal;
- (D) tarsus, tibia & genu II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.1.4 Genus *Benoinyssus* Fain

Benoinyssus Fain, 1958: 178.

DIAGNOSIS. *Benoinyssus* can immediately be distinguished from other eupodid genera by the presence of a pair of opisthosomal trichobothria in the f_1 position.

DEFINITION.

Small (218-270).

Integument: striate-spiculate, striae of prodorsal shield more densely spiculated, appendages spiculate.

GNATHOSOMA

Subcapitulum: ratio length to width 1:0.5; subcapitular setae subequal, (sbc_2) located half to three-quarters distance between (sbc_1) and anterior limit of subcapitulum.

Palp with slender tibiotarsus, ca. three times longer than widest part; supracoxal seta terminates in crown of spicules.

Chelicera: chela accounting for approximately one fifth of total length; fixed digit terminates in shallow fork; movable digit tapers suddenly in distal third; *cha* apparently smooth.

IDIOSOMA - DORSUM

Sejugal furrow clearly subdivides body into roughly triangular prodorsum and opisthosoma tapering to narrowly rounded posterior.

Naso: small lobe, rounded square or elliptical.

Setae: (iv) located on naso; (ev) located approximately fifth of distance from trichobothria to anterior limit of prodorsum; (sc) located level with

and markedly lateral to (T); respective setae of c and f row in line; all short, none reaching base of posterior seta, spinose, simple; (T) filiform, spiculated, markedly so in distal two-thirds.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-3; spinose, (a) and (b) setae slightly spatulate, remainder simple.

Genital area: four to six pairs densely spiculated eugenital setae; six pairs weakly spatulate spinose genital setae in single file or with (g_a) lateral; four to six pairs weakly spatulate spinose aggenital setae.

Anal region: anus subterminal; three pairs pseudanal setae.

LEGS.

I three-quarters of, to longer than body length, others not more than three-quarters body length; femur IV enlarged.

Setae: spinose.

Solenidia & famuli: tarsal rhagidial organs bridge-like or L-shaped, if bridge-like I & II both with one organ, if L-shaped both with two in tandem in contiguous pits; famulus of tarsus I subtending, that of II absent; tibiae I & II with one distal rhagidial organ and one proximal erect solenidion; solenidion sometimes present on genu I and tibia III.

Apotela: all of similar form.

MALE. Sperm sac clavate, unornamented.

TYPE SPECIES. *Benoinyssus najae* Fain.

DISTRIBUTION. Egypt, England, Rwanda-Burundi, Wales.

REMARKS. The presence of opisthosomal trichobothria in a eupodid was first recorded by Grandjean (1939a) who noted their presence in a taxon he identified as a species of *Eupodes*. No details were given of rhagidial organs but the length of the setae and shape of the naso resemble those of *B. ereynetoides*.

To date, the three species of *Benoinyssus* found in the British fauna are the only members of the genus.

Key to the species of *Benoinyssus*

1. Genital seta (g_1) lateral to others; one bridge-like rhagidial organ on tarsi I & II *B. ereynetoides*
- Genital setae arranged in single file; two L-shaped rhagidial organs on tarsi I & II 2
2. Leg I longer than body (ca. times 1.1); four pairs aggenital setae *B. momeni*
- Leg I shorter than body (ca. times 0.75); six pairs aggenital setae *B. najae*

Benoimyssus najae Fain

Figs 62 & 63

Benoimyssus najae Fain, 1958: 179; Fain, 1959: 358.New British record

DIAGNOSIS. *B. najae* can be distinguished from other members of the genus by the presence of respectively four and six pairs of eugenital and aggenital setae and two rhagidial organs on tarsi I and II.

Body length 247 (232-267), width 114 (108-122).

GNATHOSOMA (Figs 62C,D,E)

Subcapitulum: subcapitular setae ca. 8 long; (*sbc*₂) inserted approximately halfway between (*sbc*₁) and anterior limit of subcapitulum.

Palps: typical for genus.

Chelicerae: total length 53 (49-55); *cha* ca. 4 long.

IDIOSOMA - DORSUM (Fig. 62A)

Naso: elliptical, width approximately three times length.

Setae: (*iv*), (*ev*) subequal 17-19, (*T*) 60 (55-67), (*sc*), (*c*₁) subequal 17-20, (*c*₂), (*d*₁), (*e*₁) subequal 25-28, (*f*₁) 62-66, (*f*₂) 22-25, (*h*₁) 38-40, (*h*₂) 15-18.

IDIOSOMA - VENTER (Figs 62B,F)

Podosoma: (*1c*) at 8-10 approximately two-thirds length of (*1a & b*), (*2b*) 18-20, (*3a & b*) 12-14, (*3c & d*) 15-16, (*4a*) 10, (*4b & c*) 11-13.

Genital area: four pairs eugenital setae gradually increase in length posteriorly from 7 to 14; genital setae in single file, (g_4) 8, remainder subequal, ca. 6 long; six pairs aggenital setae, subequal ca. 10 long.

Anal region: (ps_1) 33-36, (ps_2) 14, (ps_3) 10.

LEGS (Fig. 63)

I just below body length, II and III respectively just over and just below half body length, IV just below three-quarters.

Setae: formulae - I 1-14(9+5)-11-10-22, II 1-11(6+5)-6-7-15,

III 1-8(4+4)-4-6-14, IV 1-6(3+3)-5-5-12.

Solenidia & famuli: tarsi I and II both with two dorsal rhagidial organs in tandem and in confluent pits, on I proximal ca. twice length of distal, subequal on II.

Apotela: all of similar form.

MALE. Unknown.

DISTRIBUTION. Eire, England, Rwanda-Burundi, Scotland, Wales.

MATERIAL EXAMINED. Type material: holotype ♀, RWANDA-BURUNDI, Kaninya, from mucus in nasal fossae of *Najae melanoleuca*, 2.iv.1956 [MRAC]. **British material**: ENGLAND, Suffolk, Westleton Heath, area of *Calluna* at base of slope, from aerial parts of heather plus approximately 2cm of underlying soil, 9.i.1981.

OTHER BRITISH RECORDS. EIRE, Sligo, Lough Gill, from conifer humus, 27.vi-10.vii.1971. ENGLAND, Stafford, Cannock Chase, by Great Wyrley, from bracken litter amongst silver birch, 19.ii.1982; Berkshire, Windsor

Forest, from litter inside hollow in aged oak tree, 4.i.1976 (P. D. Hillyard). SCOTLAND, Sutherland, Torboll, near Golspie, from alder carr grass and leaf litter, 29.vi.1976 (P. D. Hillyard); Strathclyde, western shore of Loch Lomond, by Edrich water, from moss, lichen and rotting wood under willow, 12.ix.1982.

REMARKS. In his description of this species, Fain (1958) infers a parasitic habit due to its occurrence in the nasal fossae of a snake. Although such habitats were not investigated in this study, the presence of large numbers of *B. najae* in litter samples suggests that Fain's find was accidental.

Examination of the type material of *B. najae* proved Fain's (1958) description of three setae on coxa III and seven pairs on the genital shields to be incorrect. It also enabled the solenidiotaxy described above to be discerned. Fain did not deal with this aspect until a subsequent paper (Fain 1959) and his figures lack the famulus on tibia I and a rhagidial organ on tarsus II.

Fig. 62. *Benoinyssus najae*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial;
- (F) genital area ♀, sagittal.

Scale intervals 10 μ m.

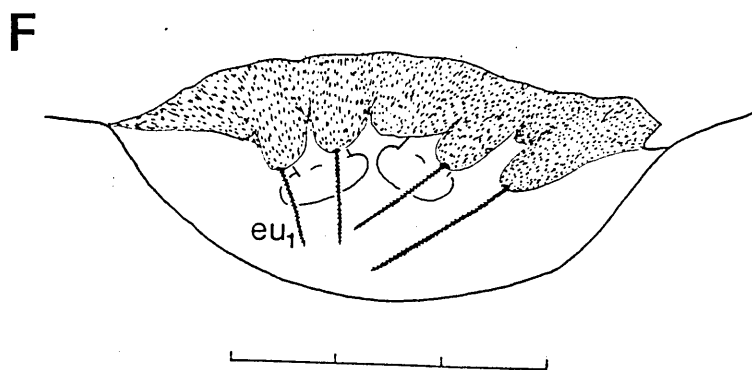
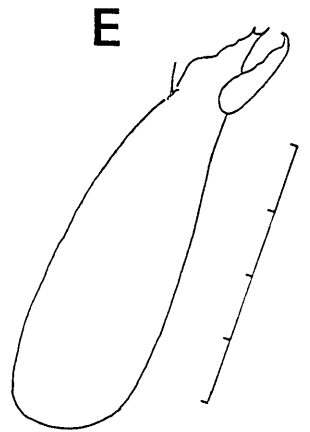
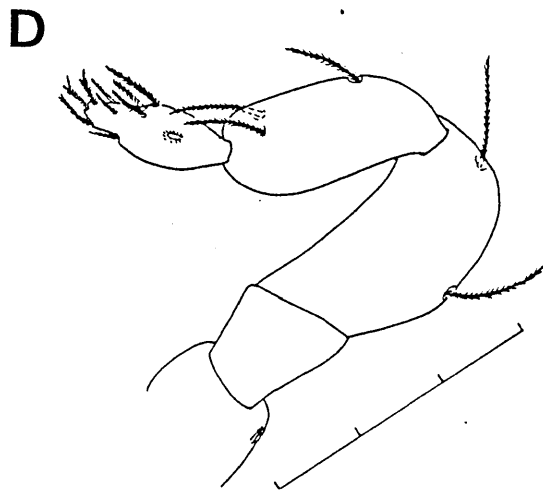
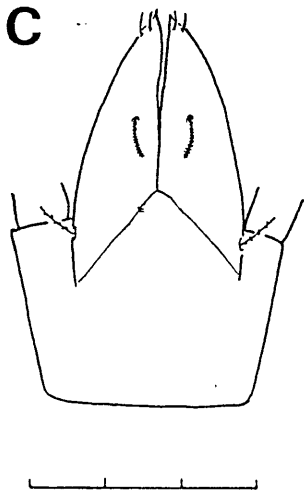
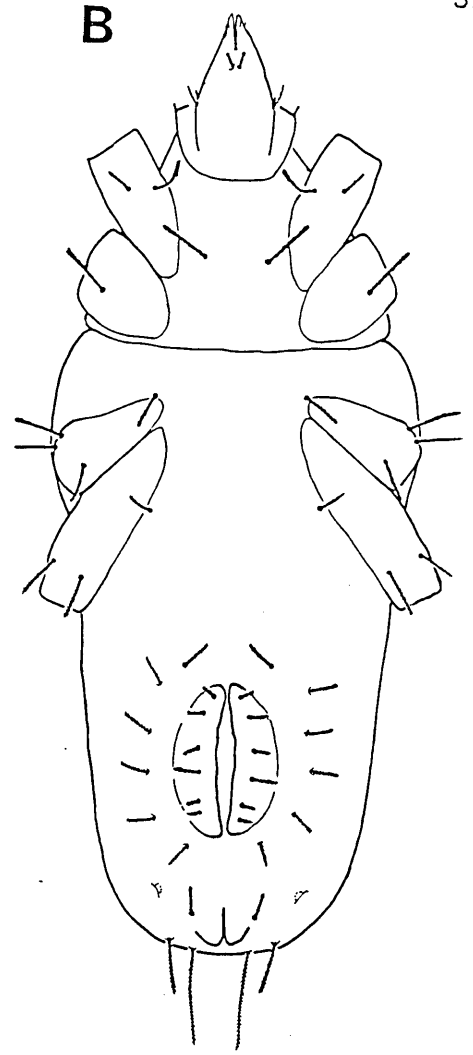
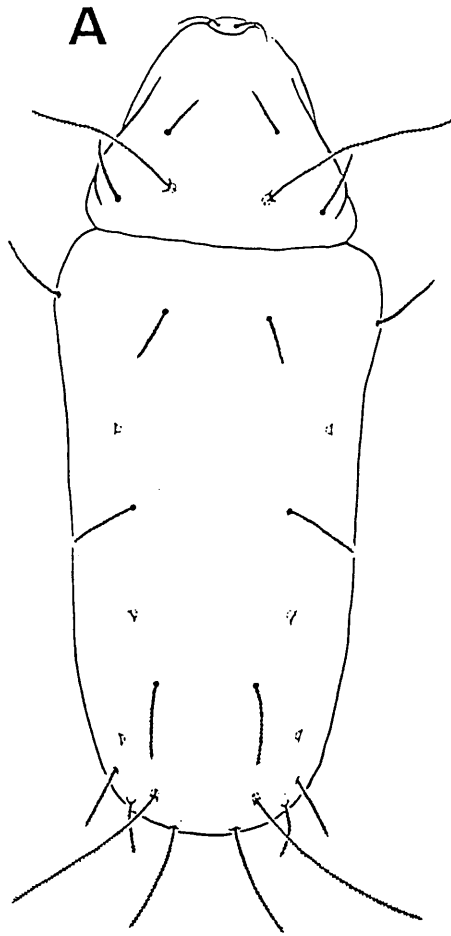
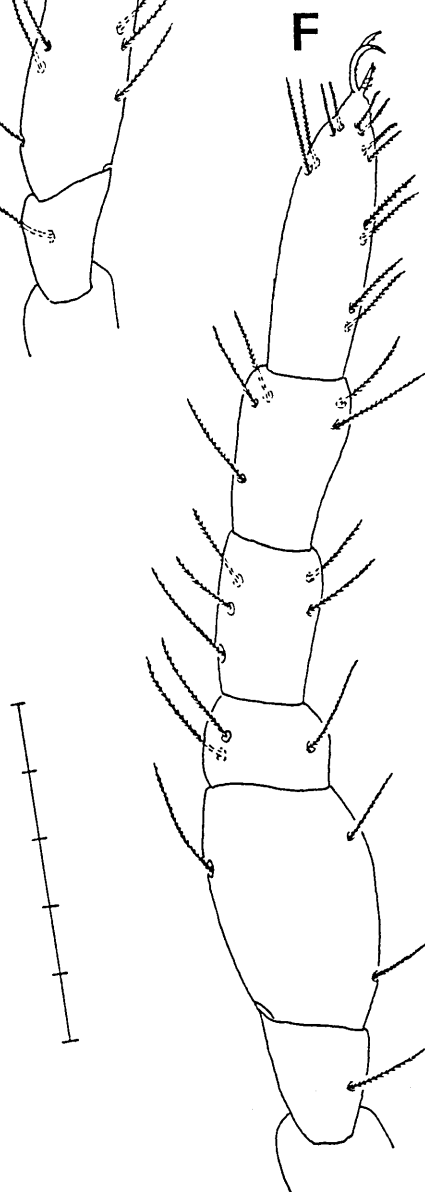
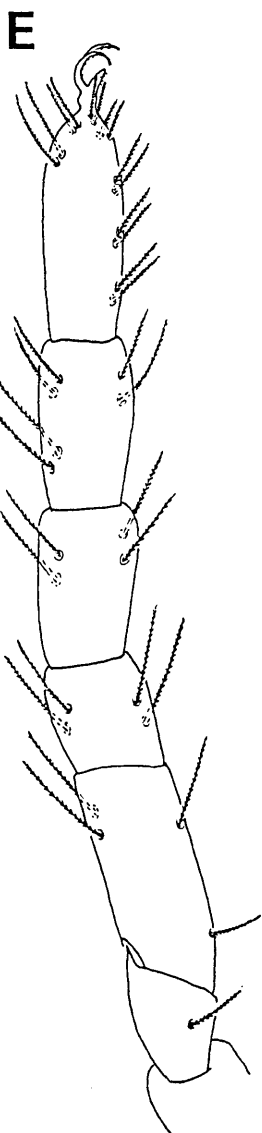
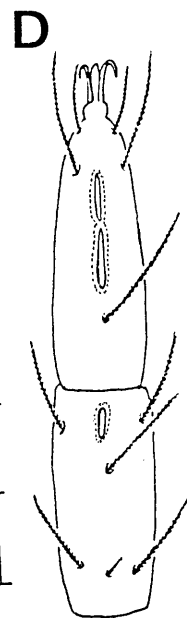
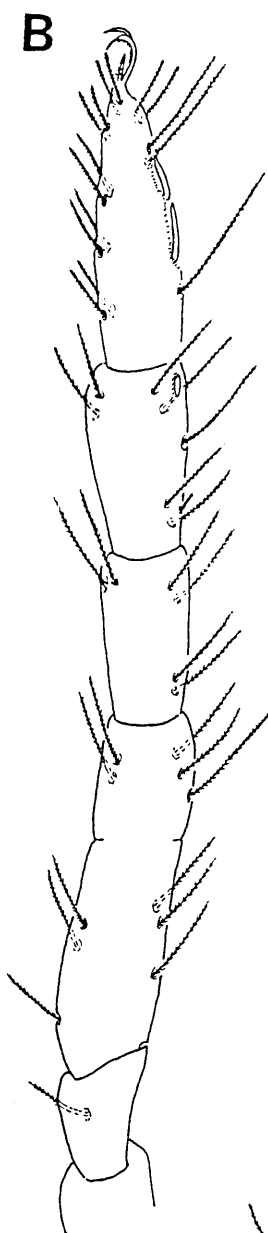
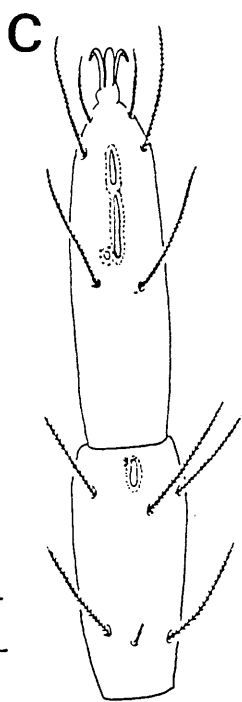
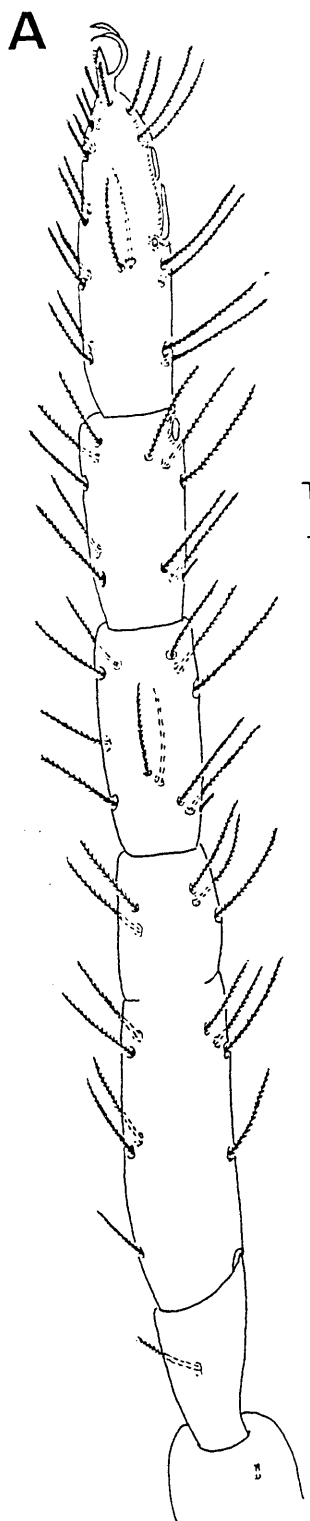


Fig. 63. *Benoinyssus najae*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Benoinyssus ereynetoides (Strandtmann & Prasse) n.comb.

Figs 64 & 65

Eupodes ereynetoides Strandtmann & Prasse, 1976: 2.New British record

DIAGNOSIS. *B. ereynetoides* can immediately be distinguished from the other members of the genus by the presence of a bridge-like rhagidial organ on tarsi I and II, the rounded square naso and (g_1) being located lateral to the other genital setae.

Body length 223 (218-231), width 118 (93-123).

GNATHOSOMA (Fig. 64B)

Subcapitulum: subcapitular setae ca. 8 long; (sbc_2) inserted three-quarters of distance between (sbc_1) and anterior limit of subcapitulum.

Palps: typical for genus.

Chelicerae: total length 48 (47-49); cha 3-4 long.

IDIOSOMA - DORSUM (Fig. 64A)

Naso: clearly delimited rounded rectangular.

Setae: (iv) 4-6, (ev) 14-15, (T) 46-49, (sc) 15, (c_1) 10-11, (c_3) 15, (d_1) & (e_1) 11-13, (f_1) 44-45, (f_2) 16-17, (h_1) 28-32, (h_2) 12-14.

IDIOSOMA - VENTER (Fig. 64B)

Podosoma: ($1a$) at 11 approximately two-thirds of ($1b$) and twice length of ($1c$) ($2b$) 14, ($3a-d$) gradually increase in length distally from 11-14, ($4a-c$) from 11-13.

Genital area: six pairs eugenital setae increase in length posteriorly from 5-8; genital setae (g_1) 9, remainder subequal ca. 6-7; five pairs

aggenital setae (ag_{1-3}) subequal at 9-10 long, (ag_4 & s) slightly shorter, ca. 7-8 long.

Anal region: (ps_1) 23-25, (ps_2) 11-14, (ps_4) 8-10.

LEGS (Fig. 65)

I just below three-quarters body length, II, III just over half body length, IV just shorter than I; femur IV enlarged.

Setae: formulae - I 1-13(8+5)-8-8-18, II 1-10(5+5)-4-6-13,

III 1-8(4+4)-4-5-12, IV 1-6(3+3)-5-5-13.

Solenidia & famuli: rhagidial organ of tarsus I in distal half of segment, curved with two attachment points; rhagidial organ of II like that of I, occupies distal two-thirds of segment; genua I and II with dorsal erect solenidion respectively one quarter and just under half distance from proximal margin of segment; tibia III with proximal posterolateral rhagidial organ just under halfway from proximal margin of segment.

MALE. (Fig. 64C) (2 specimens examined). Sperm sac clavate, unornamented.

DISTRIBUTION. England, German Democratic Republic, Scotland, Wales.

MATERIAL EXAMINED. Type material: holotype ♀, GERMAN DEMOCRATIC REPUBLIC, Etzdorf/Saalkreis Experimental Station, 0 to 10cm soil depth, summer months (MLU, slide no. 1011). British material SCOTLAND, Tayside, Rannoch Moor, approximately halfway between Rannoch Station and western end of Loch Rannoch, from litter collected between birch tree roots, 15.ix.1982. ENGLAND, Suffolk, Dingle Little Hill, approximately 2km SW of Walberswick, from top 4cm of litter under gorse.

OTHER BRITISH RECORDS. ENGLAND, Berkshire, Windsor Forest, from litter inside hollow oak, 4.i.1976 (P. D. Hillyard); Somerset, West Bagborough, woodland 500m north of Bagborough House, moss covering rotten oak branch lying on wood floor, 12.ix.1981; Kent, Westbere Marshes, approximately 5km NE of Canterbury, moss between *Phragmites* approximately 10m from western edge of lake. WALES, Dyfed, Rheidol Forest, bracken at edge of forest, from bracken litter plus approximately 4cm of underlying soil, 26.ii.1981.

REMARKS. In their description of *B. ereynetoides*, Strandtmann & Prasse (1976) illustrated the presence of seven pairs of genital setae, the fourth pair being lateral to the remainder which are arranged in single file along the free margin of the genital shields. Examination of the holotype, however, revealed only five pairs of setae along the margins of the shields, hence, a total of only six could be discerned. A complement of six pairs of genital setae was also found in all British material examined.

Fig. 64. *Benoinyssus ereynetoides*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area ♂, sagittal;

Scale intervals 10µm.

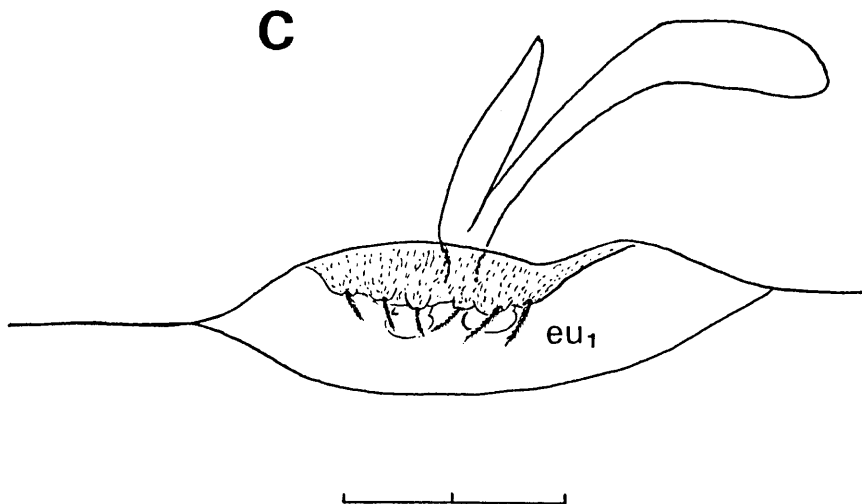
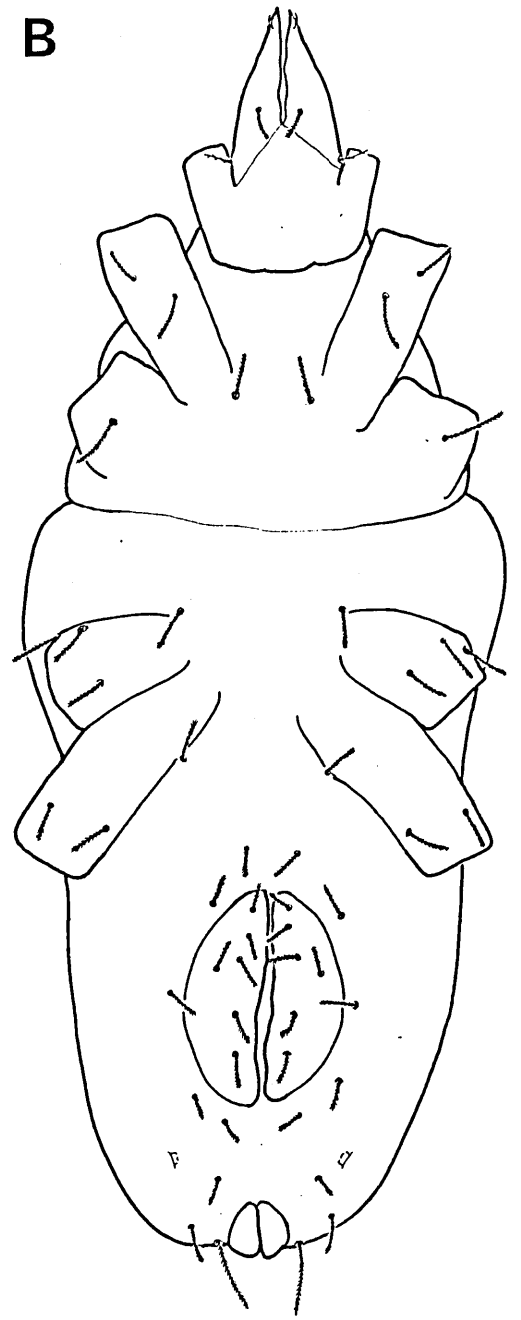
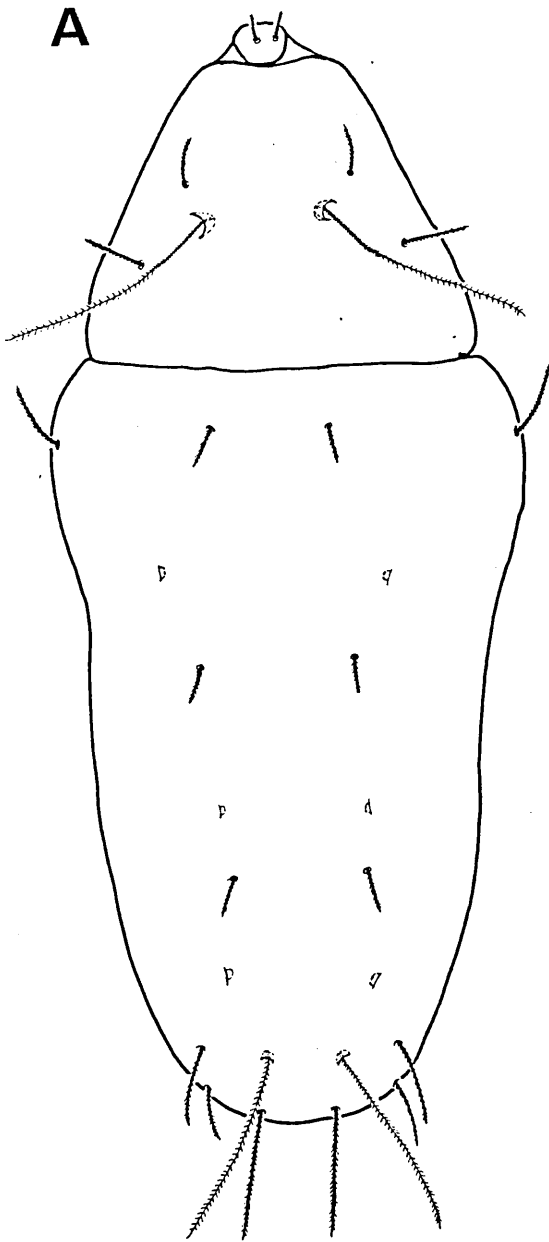


Fig. 65. *Benoinyssus ereynetoides*:

(A) leg I, posterolateral, with rhagidial organ (ω) enlarged;

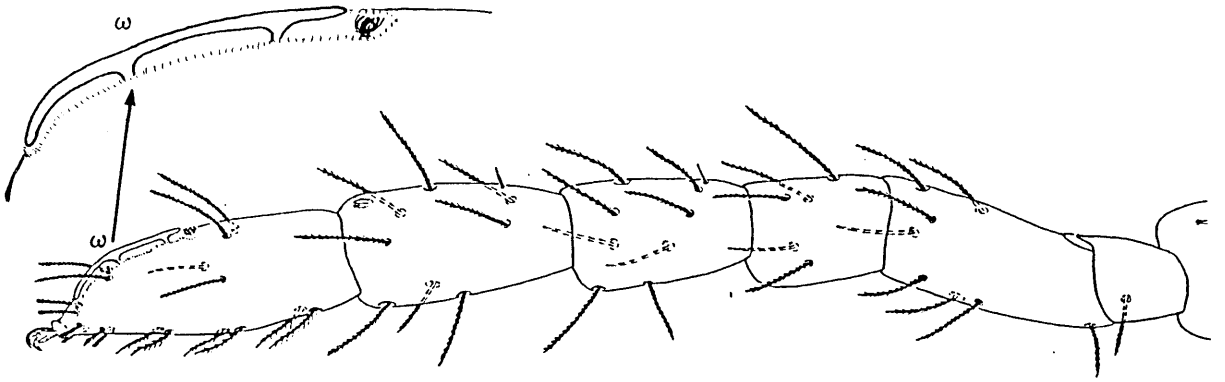
(B) leg II, posterolateral;

(C) leg III, anterolateral;

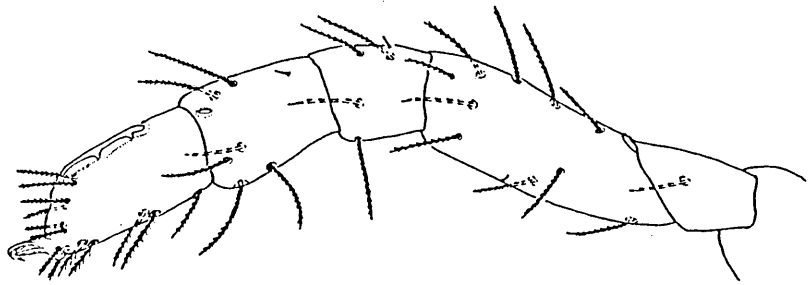
(D) leg IV, anterolateral.

Scale intervals 10 μ m.

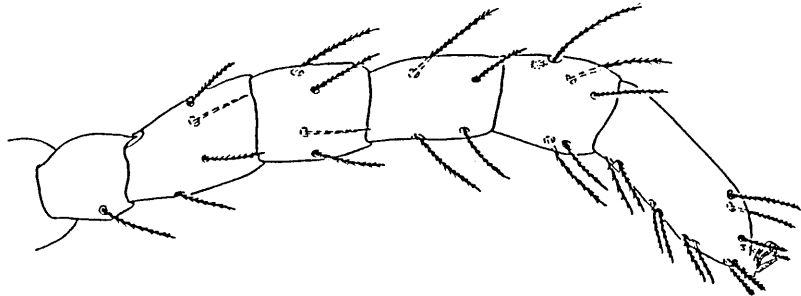
A



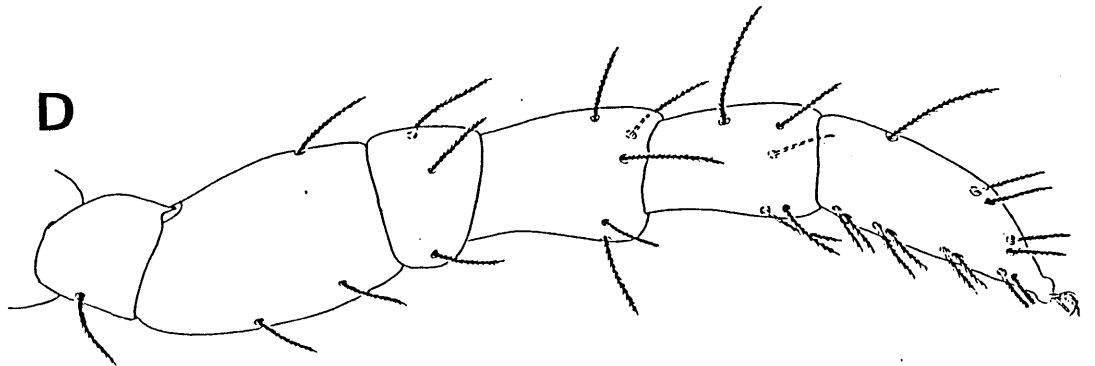
B



C



D



Benoinyssus momeni (Abou-Awad) n.comb.

Figs 66 & 67

Eupodes momeni Abou-Awad, 1984: 33.New British record

DIAGNOSIS. *B. momeni* can be distinguished from the other members of the genus by the presence of respectively five and four pairs of eugenital and aggenital setae and a rhagidial organ on genu I.

Body length 242 (227-251), width 142 (130-149).

GNATHOSOMA (Fig. 66B)

Subcapitulum: subcapitular setae ca. 9 long; (*sbc*₂) inserted approximately midway between (*sbc*₁) and anterior limit of subcapitulum.

Palp: typical for genus.

Chelicerae: total length 56 (53-59); *cha* 3 long.

IDIOSOMA - DORSUM (Fig. 66A)

Nasq: elliptical, width three times length, with delimiting suture.

Setae: extend approximately half intersetal distance; lengths - (*iv*), (*ev*), (*sc*, (*c*₁) subequal ca. 19 (17-21), (*T*) 45 (42-49), (*c*₂, (*d*₁), (*e*₁), (*f*₂) subequal ca. 25 (23-27), (*f*₁) 52 (48-55), (*h*₁) 35 (32-38).

IDIOSOMA - VENTER (Figs 66B,C)

Podosoma: *1c* at 8 long approximately two-thirds length of *1a* & *b*, *2a* 19, *3a* 8, *3c-d* and *4a-c* gradually increase in length from, respectively, 13-16 and 11-14.

Genital area: five pairs eugenital setae, subequal ca. 6 long; genital setae in single file, subequal ca. 8 long; four pairs aggenitals gradually decrease in length posteriorly from ca. 13-10.

Anal region: (ps_3) 10 long, (ps_2) at 14 approximately third length of ps_1).

LEGS (Fig. 67)

I just longer than body, II and III just below half, IV approximately three-quarters body length.

Setae: formulae I 1-14(9+5)-8-9-18, II 1-11(6+5)-7-8-15, III 1-8(4+4)-5-6-12, IV 1-7(4+3)-4-5-12.

Solenidia & famuli: tarsi I and II both with two rhagidial organs; genu I with dorso-distal rhagidial organ.

MALE. Unknown.

DISTRIBUTION. Egypt, England, Scotland, Wales.

MATERIAL EXAMINED. Type material: holotype ♀, EGYPT, El-qaliubiya region, from litter (F. M. K. Momen) [PPL]. British material: ENGLAND, Cambridgeshire, near Peterborough, Spring Close, from hedgerow litter, 23.i.1978 (P. N. Lawrence & B. R. Pitkin).

OTHER BRITISH RECORDS. ENGLAND, Oxfordshire, Wytham Woods, from top 4cm of beech litter, 26.iv.1982; Suffolk, Dingle Great Hill, east slope, at border of patch of heathland, from mixed *Agrostis*, *Cladonia* and *Pleurozium schreberi* plus top 2cm of underlying soil, 7.i.1981. SCOTLAND, Highland, Benn Eighe, 700m along nature trail, from *Sphagnum* and *Polytrichum* moss amongst heather, 16.ix.1982; Strathclyde, Inchcailloch, main

island in Loch Lomond, from oak litter, grass and spleenworts, 13.ix.1982.

WALES, Dyfed, Rheidol Forest, from hemlock litter, 26.ii.1981.

REMARKS. In his description of this species, Abou-Awad (1984) illustrates only one rhagidial organ on both tarsi I and II but examination of type material confirmed the presence of two.

Fig. 66. *Benoinyssus momeni*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area ♀, sagittal;

Scale intervals 10µm.

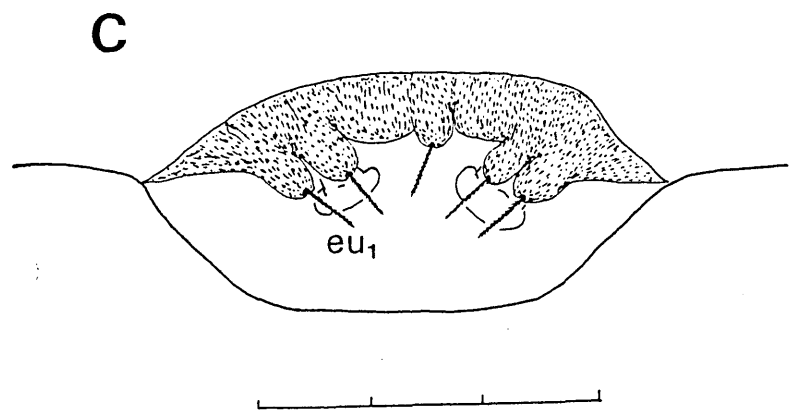
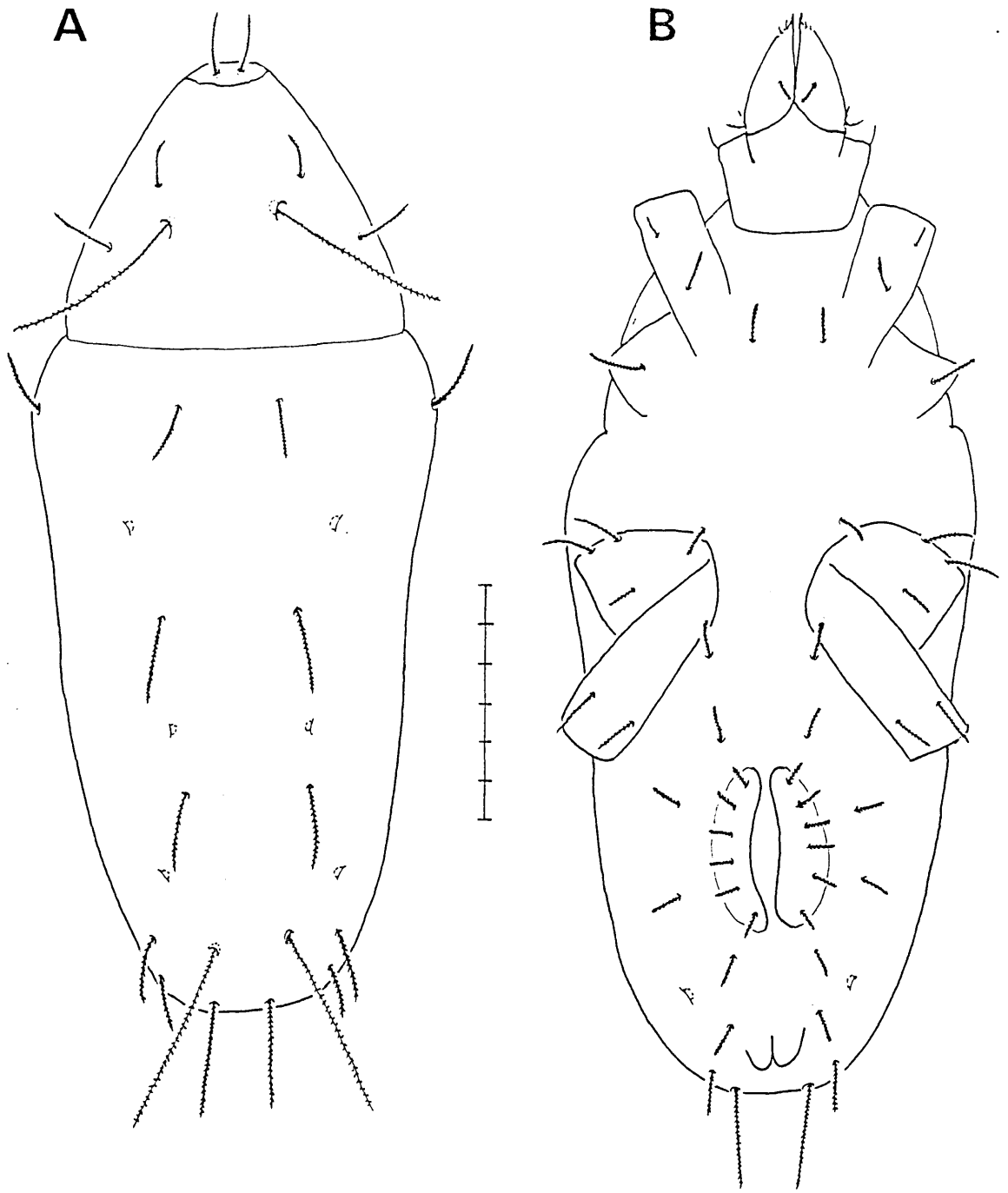
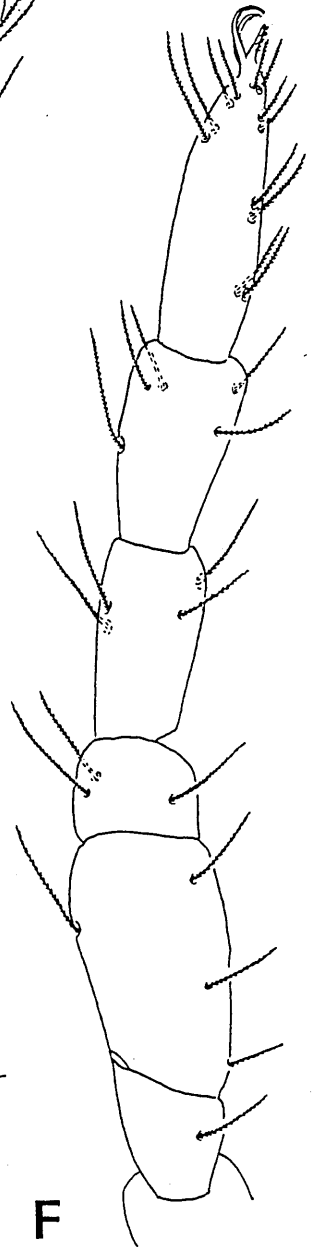
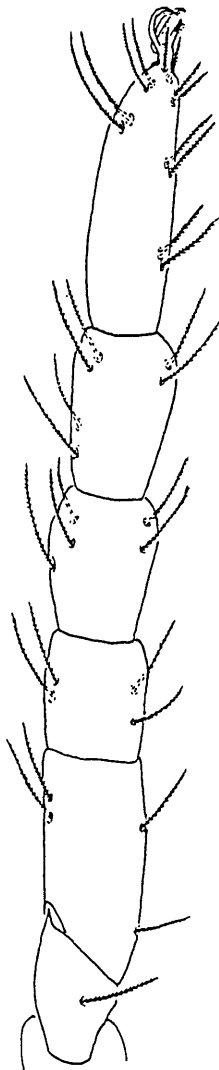
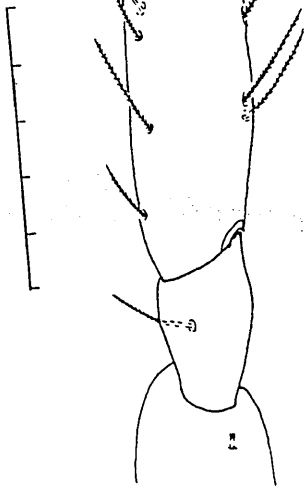
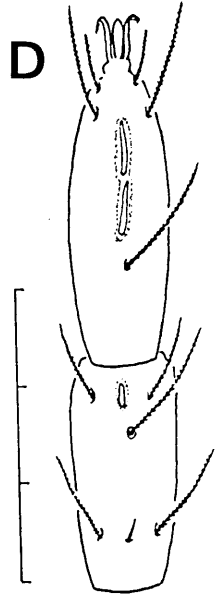
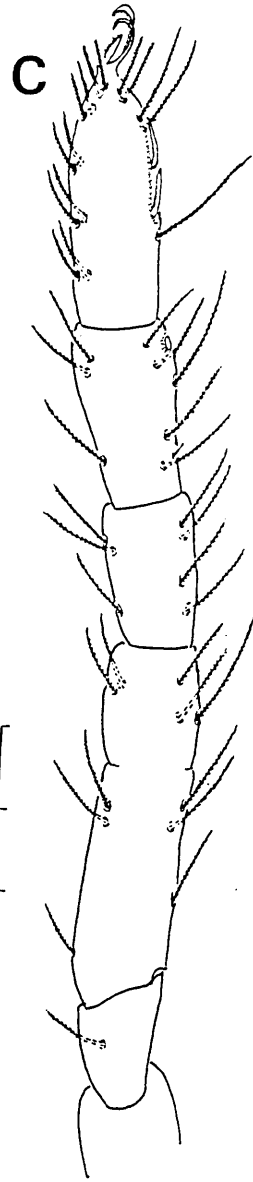
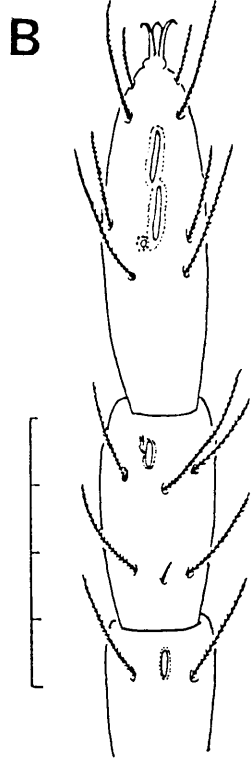
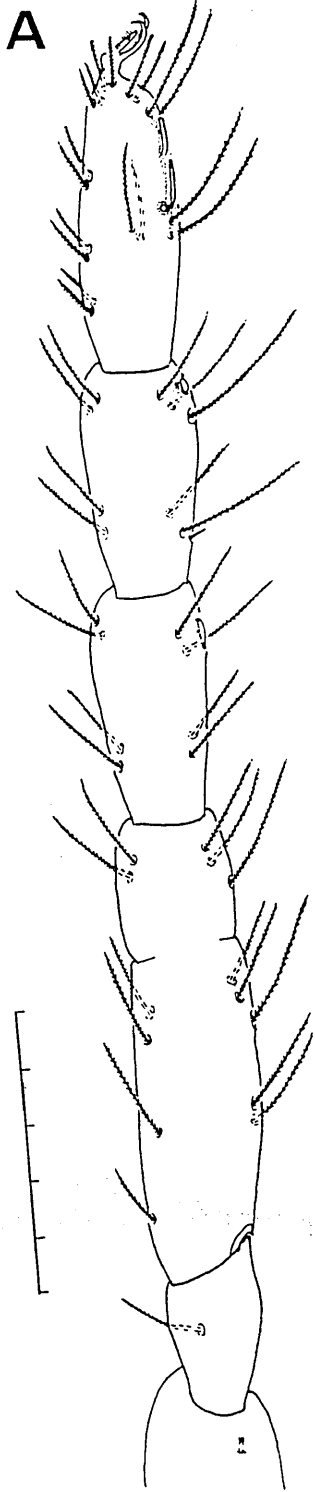


Fig. 67. *Benoinyssus momeni*:

- (A) leg I, posterolateral;
- (B) tarsus & tibia I, dorsal;
- (C) leg II, posterolateral;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



E

F

10.1.1.5 Genus *Caleupodes* n.gen.

DIAGNOSIS. *Caleupodes*, known only from the type species, can be distinguished from other eupodid genera by the presence of external evidence of primary opisthosomal segmentation in the form of transverse furrows of differentiated integument.

DEFINITION.

Small (300-330).

Integument: conspicuously ornamented, predominantly with reticulations of papillae or spicules linked by fine striae; prodorsal shield absent; apart from over sejugal furrow and segmental boundaries, some papillae enlarged, forming a second network.

Opisthosoma divided into segments dorsally by transverse furrows of differentiated integument.

GNATHOSOMA

Subcapitulum: ratio length to width ca. 1:0.5; (sbc_1) markedly shorter than (sbc_2), latter inserted ca. midway between (sbc_1) and anterior limit of subcapitulum.

Palps with slender tapering tibiotalrus, length ca. three times greatest width; supracoxal setae terminate in crown of blunt spicules.

Chelicerae: chela account for approximately one fifth of total length; fixed digit terminates in shallow fork; movable digit narrows suddenly to slender part in distal third; *cha* smooth.

IDIOSOMA - DORSUM

Sejugal furrow clearly subdivides body into roughly triangular prodorsum and opisthosoma with shoulders narrowing to rounded posterior.

Naso blunt, not delimited dorsally, appears as overhanging lobe in lateral view.

Setae: (*iv*) located at anterior of naso; (*ev*) located mid-way between (*T*) and anterior limit of prodorsum; (*sc*) level with and markedly lateral to (*T*); setae of *c* and *f* row in line; all short, extending approximately a third of distance to base of posterior seta; (*T*) filiform, spiculated, markedly so in distal two-thirds, other setae smooth to weakly serrate.

Lyrifissures: circular.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-3; setae simple, tapering, subequal.

Genital area with six pairs fine, tapering, spiculated eugenital setae; seven pairs genital setae, arranged in single file, and five pairs aggenitals, all simple, spinose.

Anal region: anus subterminal; two pairs pseudanal setae; (*ih*) just anterior and lateral to (*ps₃*).

LEGS.

Slender, all shorter than body, I approximately three-quarters body length.

Setae: smooth to spinose.

Solenidia & famuli: rhagidial organs L-shaped; tarsi I and II both with two dorsal rhagidial organs in tandem and in confluent pits, located respectively on distal half and median third of segment; famuli slightly posterolateral to base of ω_1 ; tibia I with famulus located posterolaterally in pit with distal rhagidial organ, one proximal rhagidial organ halfway along segment; tibia II with proximal and distal rhagidial organ.

Apotela: all of similar form.

MALE. Unknown.

TYPE SPECIES. *Caleupodes reticulatus* n.sp.

DISTRIBUTION. England.

ETYMOLOGY. The name is derived from the Greek 'calos' meaning beauty.

REMARKS. The dimensions, the short setae, the slender femora IV and the single row of genital setae as seen in *Caleupodes* agree most closely with the characters of the now invalid genus *Protereunetes* Berlese (Fain 1964, Strandmann 1970). *Caleupodes*, however, differs by lacking a distinct naso and by possessing two and not three pairs of pseudanal setae. The species of the genus *Cocceupodes* Thor possess two pairs of pseudanal setae and a naso that is not clearly delimited dorsally. *Caleupodes*, by contrast, lacks the swollen femora IV and the T-shaped rhagidial organs found in *Cocceupodes*, while the internal vertical setae are located on the naso and not posterior to it.

Caleupodes reticulatus n.sp.

Figs 14e, 17a,b,f, 18g, 19d, 21a,b, 22e, 23f, 25a, 68 & 69

Body length 313 (300-330), width 152 (141-163) (7 specimens examined).

GNATHOSOMA (Figs 22e, 23f, 68C,D,E)

Subcapitulum: (*sbc*₁) at 4.5 long, approximately half length (*sbc*₂).

Palp: femoral seta *d*; smooth, much shorter than other spinose, setae.

Chelicerae: total length 70 (67-72); *cha* 4 long.

IDIOSOMA - DORSUM (Figs 14e, 17a, 21a, 68A)

Setae: (*iv*) 14 long, (*sc*) 16, (*ev*) distinctly shorter than others at 8, setae increase gradually in length from *c* row, ca. 15 to *h* row, ca. 18; all fine, taper to point, appear smooth under light microscope, though SEMs show (*ev*) to be ridged, the remainder weakly serrated, increasing in degree from (*iv*) to *h* setae.

IDIOSOMA - VENTER (Figs 21b, 25a, 68B,F)

Podosoma: setae spinose, simple, increase in length distally on I, III and IV from ca. 10 to 15 long, (*2a*) 13.

Genital area: *eu*₂ slightly lateral, ca. 10 long, other eugenital setae subequal, 13-15; genital and aggenital setae subequal ca. 10; four gravid females, three with single egg, one with two, all eggs reniform, ca. 120 long.

Anal region: (*ps*₁) 13, weakly serrate, same form as dorsal setae; (*ps*₂) 10, spinose, like ventral setae.

LEGS (Figs 17b,f, 18g, 19d, 69)

I approximately three-quarters body length, II and III just below half body length, IV just above; in lateral aspect, tarsus I with dorsal 'step' about halfway along length.

Setae: formulae I 1-13(8+5)-11-12-18, II 1-10(5+5)-4-5-12, III 1-7(3+4)-4-5-11, IV 1-6(3+3)-6-5-10; all moderately short; tarsal setae spinose, on other segments ventral setae spinose, laterals spinose or weakly serrated, dorsals weakly serrated.

Solenidia & famuli: proximal solenidion of tibiae minute, in circular pit about halfway along segment.

MALE. Unknown.

ETYMOLOGY. The specific name refers to the reticulate ornamentation of the integument.

DISTRIBUTION. England.

MATERIAL EXAMINED. Holotype ♀, ENGLAND, Suffolk, Hollesley Common, from rotten pine stump, 7.iii.1964 (P.N. & K. Lawrence)[BMNH, reg.no. 1985.7.2.11]. Paratypes 6♀♀, same data as holotype [BMNH, reg.nos 1985.7.2.2-7].

REMARKS. The discovery of *C. reticulatus* enabled the association of opisthosomal segments, setae and lyrifissures to be established in the Eupodoidea (for more details see section 11). In addition, the different forms of the dorsal and ventral opisthosomal setae help to illustrate the 'caudal bend', as discussed by Sitnikova (1978), since pseudanal setae (ps_1) are of the dorsal kind, while (ps_3) are like those found ventrally.

Fig. 68. *Caleupodes reticulatus* n.sp.:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) chelicera, antiaxial;
- (E) palp, antiaxial;
- (F) genital area ♀, lateral.

Scale intervals 10µm.

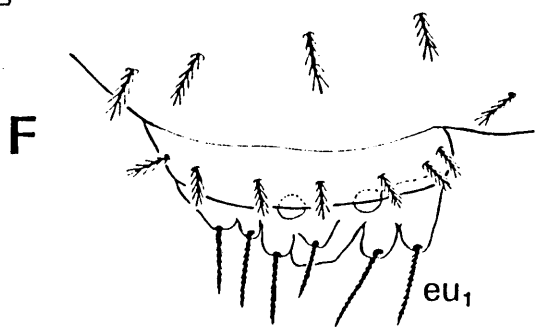
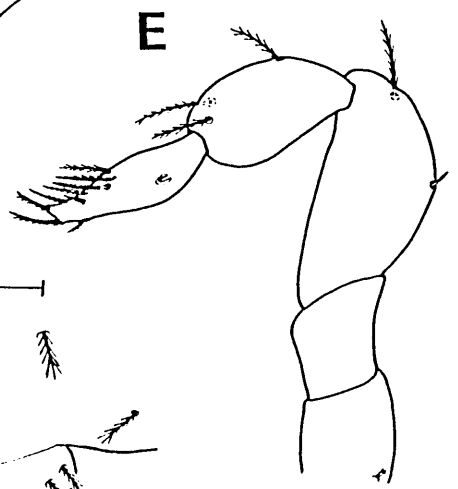
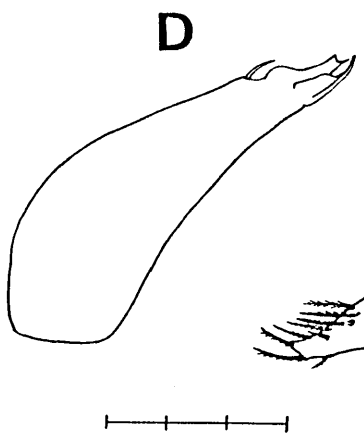
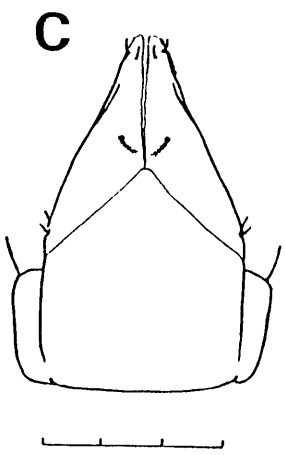
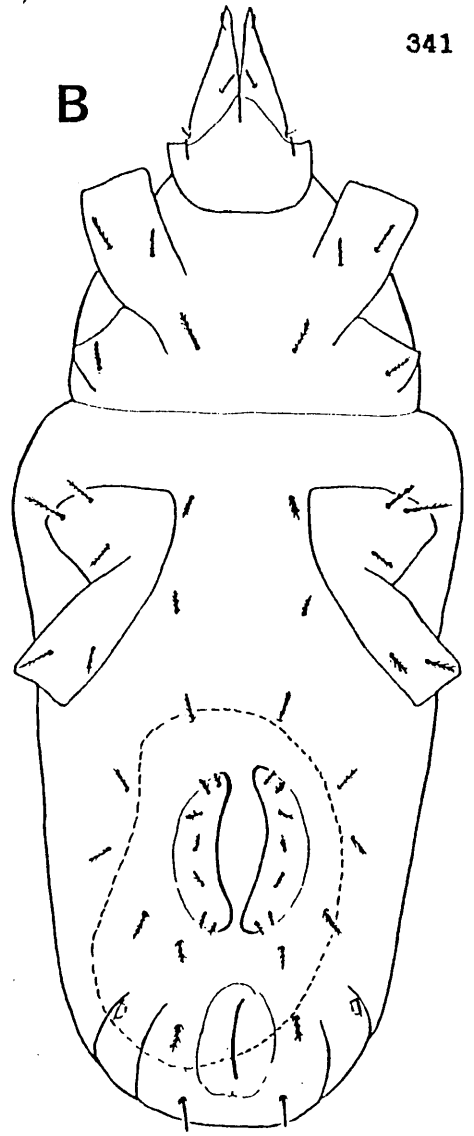
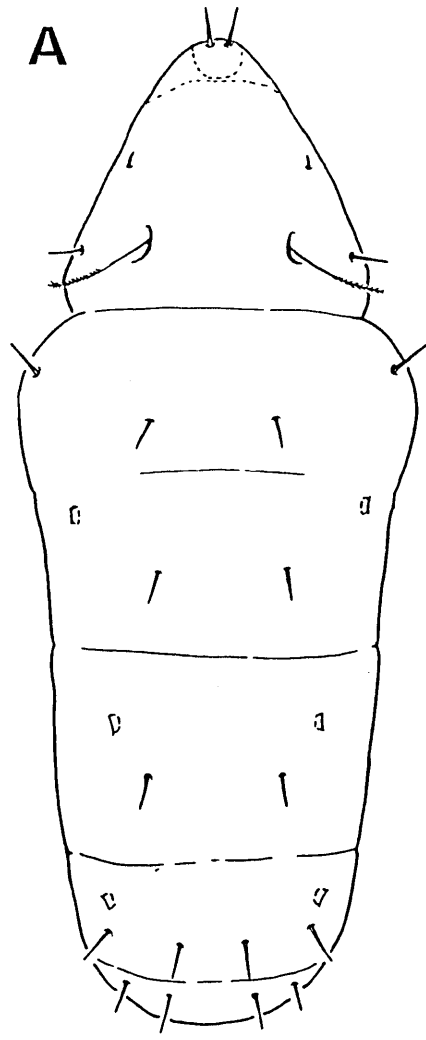
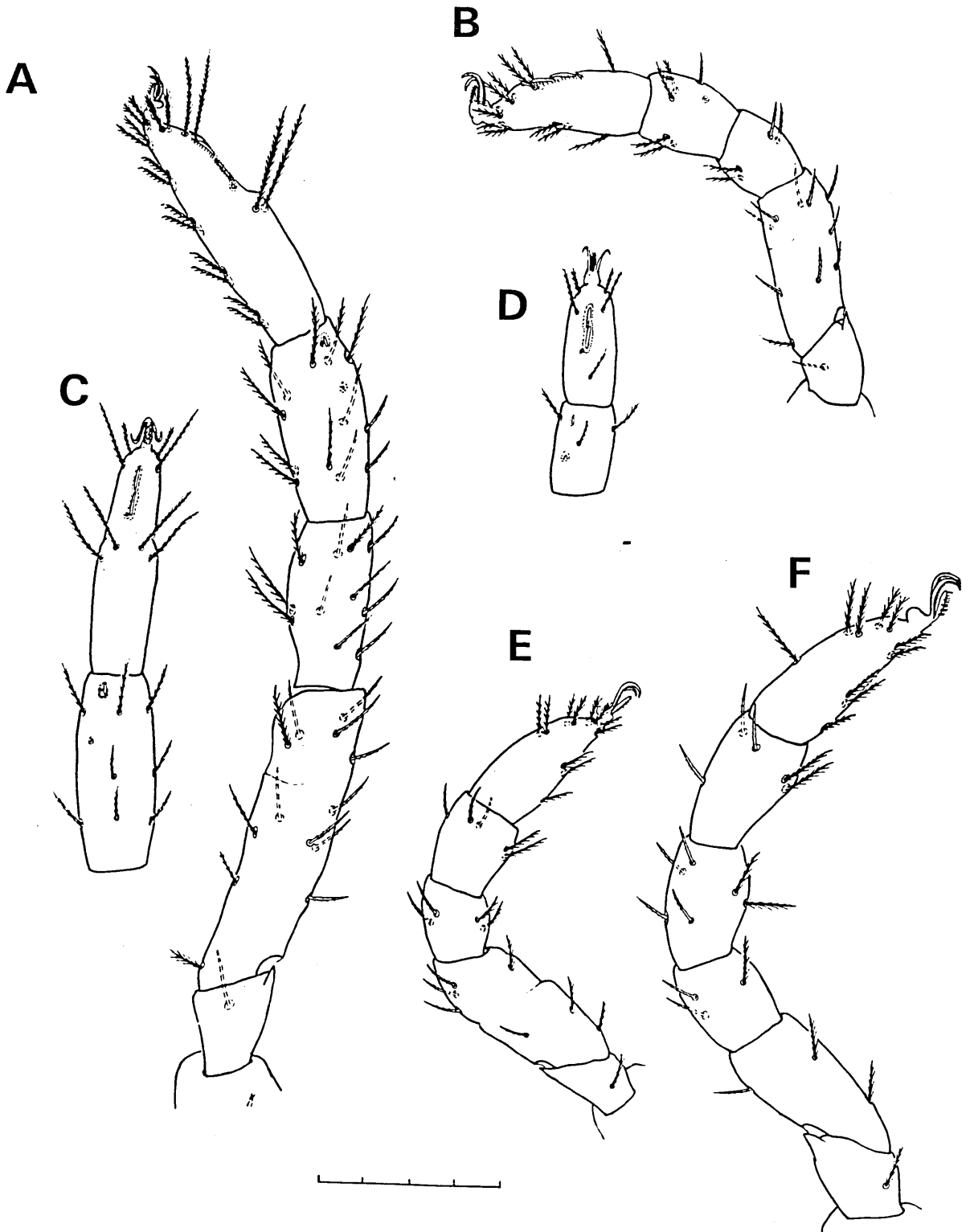


Fig. 69. *Caleupodes reticulatus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.1.6 Genus *Claveupodes* Strandtmann & Prasse

Claveupodes Strandtmann & Prasse, 1976: 10.

DIAGNOSIS. Can immediately be distinguished from all other eupodid genera by the expanded (subclavate or clavate) prodorsal trichobothria and the position of opisthosomal setae (f_2) posteriorly and just laterally to (f_1).

DEFINITION.

Small (174-205).

Integument: weakly to strongly striate-spiculate; prodorsal shield papillate or with striae more densely spiculed than surrounding integument; appendages spiculed.

GNATHOSOMA

Subcapitulum: ratio length to width 1:0.6; (sbc_1) ca. two-thirds length (sbc_2), latter located ca. third to quarter of distance between (sbc_1) and anterior limit of subcapitulum.

Palps with ovoid tarsus, length approximately twice width; supracoxal seta minute, apparently not ornamented.

Chelicerae: chela account for approximately one fifth of total length; flexed ventrally; fixed digit terminates in shallow fork; movable digit narrows suddenly to slender part in distal third; *cha* smooth.

IDIOSOMA - DORSUM

Sejugal furrow clearly divides body into roughly triangular prodorsum and slightly shouldered opisthosoma gradually tapering to rounded posterior.

Naso inconspicuous, visible in lateral view as slight extension of prodorsum.

Setae: (*iv*) located at base of naso; (*ev*) just lateral to (*T*), approximately quarter of distance from them to anterior limit of prodorsum; (*T*) located just anterior to markedly sublateral (*sc*); *c* row in line; (*f₂*) posterior and just lateral to (*f₁*); (*T*) subclavate or clavate, spiculated, inserted in deep, wide-mouthed bothridium; remaining setae simple, spinose, short.

Lyrifissures: eye-like.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-3; setae simple, spinose.

Genital area: three pairs fine, tapering, spiculated eugenital setae; four pairs genital setae, arranged in single file, and four pairs aggenitals, all simple, spinose.

Anal region: anus terminal, visible in dorsal view; three pairs spinose pseudanal setae; (*ps₁*) just dorsal, (*ps₂*) subterminal, (*ps₃*) ventral; (*ih*) just anterior but markedly lateral to (*ps₃*).

LEGS.

Slender, all shorter than body, I just over half body length.

Setae: spinose.

Solenidia & famuli: rhagidial organs I-shaped, sometimes expanded; two rhagidial organs more or less dorsally on tarsi I and II and slightly posterolaterally on tibiae I and II; famuli slightly posterolateral to base of ω_1 ; famulus of tibia II located posterolaterally in pit with rhagidial organ; solenidion sometimes present on tibia III.

Apotele: all of similar form.

MALE. Unknown.

TYPE SPECIES. *Claveupodes delicatus* Strandtmann & Prasse

DISTRIBUTION. England, German Democratic Republic, Wales.

REMARKS. The members of *Claveupodes* most closely resemble those of *Subeupodes* n.gen. in the number of rhagidial organs and pseudanal setae. They differ, however, by the expanded form of the prodorsal trichobothria and the inconspicuous naso with the internal vertical setae located at its base. Although certain species of *Cocceupodes* lack a delimited naso, the internal verticals are clearly inserted posterior to it, while the prodorsal trichobothria are always filiform and three setae on coxa IV and two pairs of pseudanal setae are present.

To date, the three species found in the British fauna are the only members of the genus.

Key to the species of *Claveupodes*

1. Idiosoma heavily and conspicuously striated; tibia III without small rhagidial organ *C. ornatus* n.sp.
- Idiosoma weakly and inconspicuously striated; tibia III with small rhagidial organ 2
2. (*T*) subclavate; rhagidial organs of tarsus I subequal, not greatly enlarged; dorsal genual seta of palp spinose *C. delicatus*
- (*T*) clavate; rhagidial organs of tarsus I enlarged, proximal twice the size of distal; dorsal genual seta of palp smooth *C. juvenalis* n.sp.

Claveupodes delicatus Strandtmann & Prasse

Figs 70 & 71

Claveupodes delicatus Strandtmann & Prasse, 1976: 11.New British record

DIAGNOSIS. Differs from other species of *Claveupodes* by being inconspicuously ornamented and possessing subclavate trichobothria and slender rhagidial organs.

Body length 203 (192-211), width 97 (94-101).

GNATHOSOMA (Fig. 70C,D,E)

Subcapitulum: (*sbc*₂), ca. 3.5, inserted third distance from (*sbc*₂) to anterior limit of subcapitulum.

Palp: typical for genus.

Chelicera: total length 34 (32-37); *cha* 5 long.

IDIOSOMA - DORSUM (Fig. 70A)

Setae: (*T*) subclavate, spiculed, 30 long; (*ev*), (*sc*), (*c*₃) 7 to 8 long, (*h*₁), (*h*₂) 9 to 10 long, remainder 5 to 6 long.

IDIOSOMA - VENTER (Figs 70B,F)

Podosoma: setae (*1c*), at 4 long ca. two-thirds length of (*1a* & *b*); (*2a*) 8; (*3a-d*) subequal, 6-7; (*4a-c*) subequal, 5-6.

Genital area: all setae short ca. 3.5 long; three gravid females with one large, ca. 96 long, ovoid egg.

Anal region: (*ps*₃) at 4.5 ca. two-thirds (*ps*₁ & *2*).

LEGS (Fig. 71)

I and IV just over half body length, II and III just below.

Setae: formulae I 1-9(4+5)-7-5-14, II 1-9(4+5)-4-5-12, III 1-6(3+3)-4-5-10, IV 1-5(2+3)-4-4-9; all moderately short; seta of trochantera I and II and anterolaterals of femora and genua I and II weakly serrate, remainder spinose.

Solenidia & famuli: two rhagidial organs on tarsus I, subequal, in tandem in confluent pits occupying distal half of segment, not greatly enlarged; tibia I with subequal rhagidial organs located proximally and distally; rhagidial organs on tarsus II parallel, slightly staggered, long, approximately third length of segment; tibia II with small rhagidial organs located in distal half of segment, in tandem but separate pits; tibia III with dorsobasal, semi-erect rhagidial organ.

MALE. Unknown.

DISTRIBUTION. England, German Democratic Republic, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, GDR, Eitzdorf/Saalkreis Experimental Farm, soil under grass crops, (J. Prasse) [MLU]. Paratypes 13 ♀♀, same data as holotype. British material: ENGLAND, Suffolk, rotten wood from willow tree-hole, 9.i.1981.

OTHER BRITISH RECORDS. ENGLAND, Kent, Canterbury Woods, oak and hawthorn litter under bracken, 17.iii.1981; *Pinus contorta* leaf and cone litter, 17.iii.1981; WALES, Dyfed, Capel Bangor, leaf litter under hawthorn hedge, 26.ii.1981.

REMARKS. Nine setae could be discerned on the palp tibia-tarsus of *C. delicatus* rather than the six described by Strandtmann & Prasse (1976), while the presence of three pairs of eugenital setae was confirmed.

This was a relatively uncommon species in Britain, occurring in rotten wood and leaf litter.

Fig. 70. *Claveupodes delicatus*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) palp, antiaxial;
- (D) chelicera, antiaxial;
- (E) genital area σ , ventral.

Scale intervals 10 μ m.

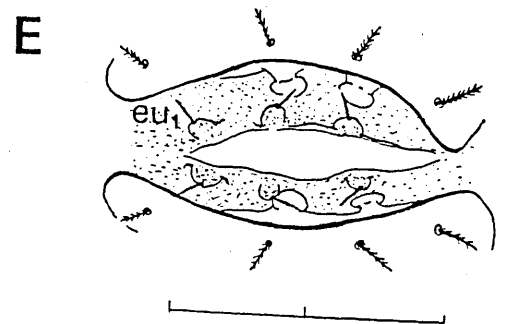
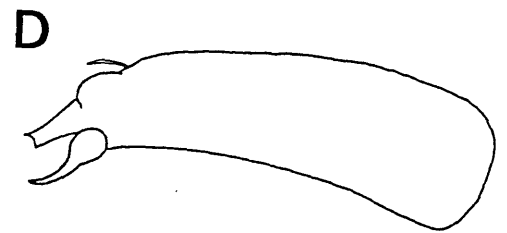
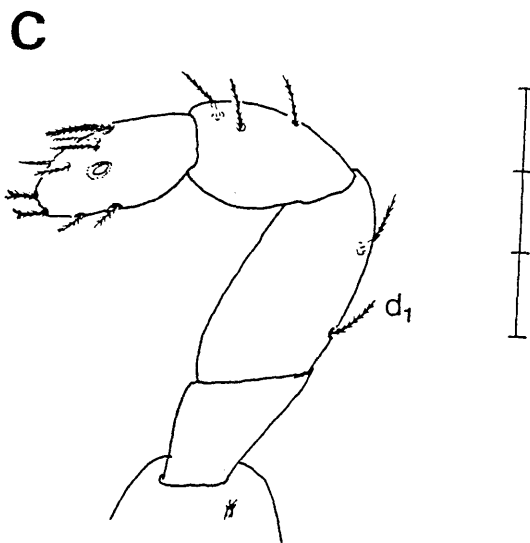
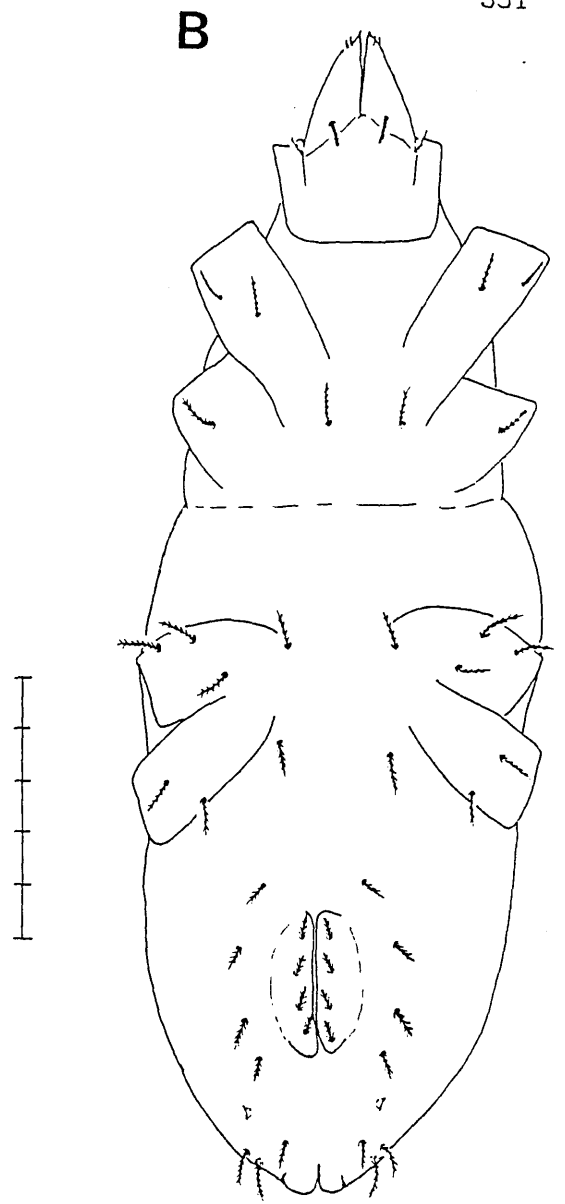
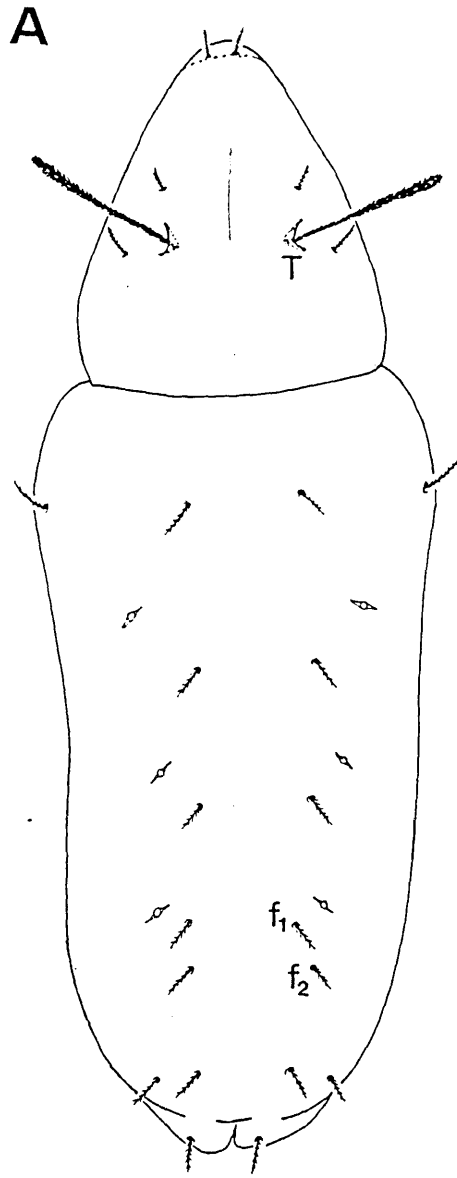
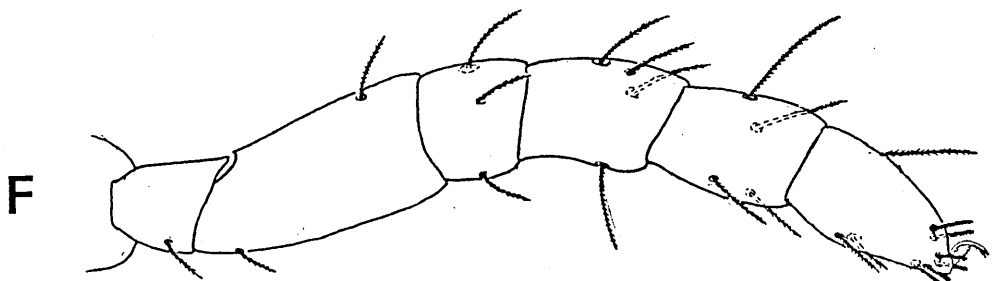
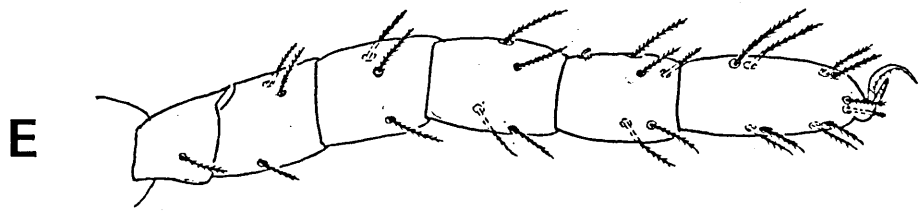
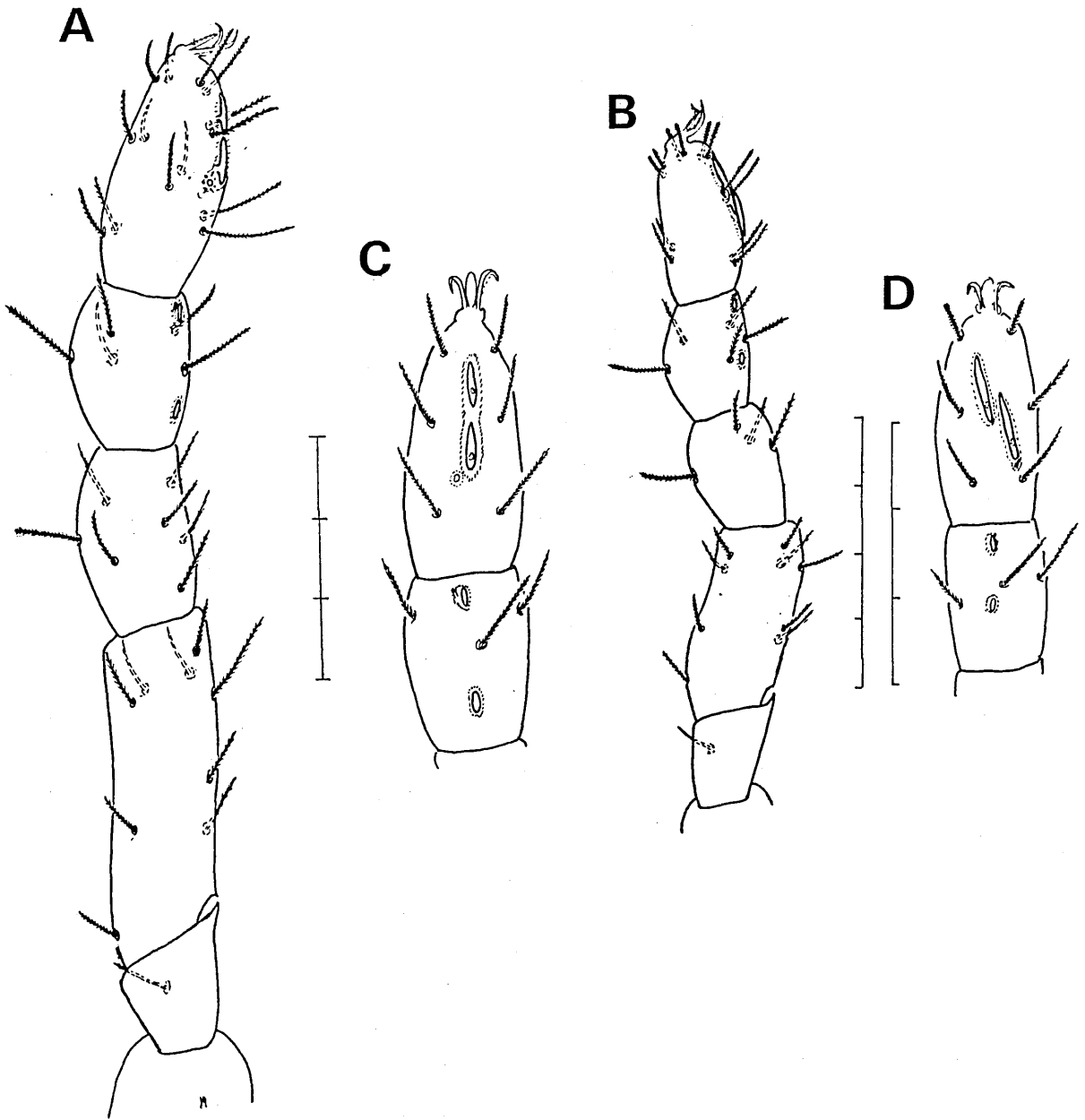


Fig. 71. *Claveupodes delicatus*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Claveupodes juvenalis n.sp.

Figs 72 & 73

DIAGNOSIS. Can be distinguished from the other species of *Claveupodes* by the weakly ornamented integument and the smooth dorsal palp genual seta.

Body length 178 (171-183), width 64 (59-67)).

GNATHOSOMA (Figs 72B,C)

Subcapitulum: (*sbc*₂) 5 long, inserted third of distance from (*sbc*₁) to anterior limit of subcapitulum.

Palp: genual seta *d* smooth; remaining setae spinose.

Chelicera: total length 32 (29-35); *cha* smooth, 5 long.

IDIOSOMA - DORSUM (Fig. 72A)

Setae: (*T*) clavate, 29 long; (*ev*), (*sc*), (*c*₂) 7 to 9 long, (*h*₁), (*h*₂) 10 to 11 long, remainder 6.

IDIOSOMA - VENTER (Figs 72B,D)

Podosoma: setae spinose, simple; (*1c*) at 5 long approximately two-thirds length of (*1a* & *b*); (*2a*) 7; (*3a-d*) subequal, 5-6; (*4a-c*) subequal, ca. 5.

Genital area: all setae short ca. 3 long, although (*g*₃ & *4*) slightly shorter; 5 gravid females each with one large 82 (75-87) long, ovoid egg.

Anal region: (*ps*₃) at 6 ca. two-thirds (*ps*₁ & *2*).

LEGS (Fig. 73)

I longest; I and IV just over half body length, II and III just below; tarsus I somewhat inflated.

Setae: formulae I 1-9(4+5)-7-5-14, II 1-9(4+5)-4-5-12,

III 1-6(3+3)-4-5-10, IV 1-5(2+3)-4-4-9; shorter than respective segment apart from *d* on tibiae which are approximately same length as segment;

seta of trochantera I and II, some ventrals and anterolaterals of femora and genua smooth or weakly serrated, remainder spinose.

Solenidia & famuli: rhagidial organs of tarsus I located in distal half of segment, proximal enlarged, tongue-shaped, approximately twice as large as distal, famulus distinct, located outside pit just posterolateral and posterior to ω_1 ; rhagidial organs of tibia I in separate pits in distal half of segment, in tandem, proximal slightly posterolateral to distal and more slender; organs parallel on tarsus II, more proximal extends nearly length of segment, distal approximately half its length; those of tibia II with similar arrangement to those of I but organs about half their size; tibia III with small, semi-erect solenidion in pit just proximal.

MALE. Unknown.

ETYMOLOGY. The specific name refers to the weak sclerotization of this species, which gives specimens an immature appearance.

DISTRIBUTION. England, Wales.

MATERIAL EXAMINED. Holotype ♀, WALES, Dyfed, Ynyslas Nature Reserve, 100m from saltmarsh, *Agrostis* sp. and underlying sandy soil, 25.ii.1981 [BMNH, reg.no. 1987.3.24.1]. Paratypes 9♀♀, same data as holotype [BMNH, reg.nos 1987.3.24.2-10].

OTHER BRITISH RECORDS. ENGLAND, Suffolk, Dingle Great Hill, east slope, sandy soil under burnt gorse bush, 7.i.1981; rotten wood from tree-hole in west side of willow tree, 9.i.1981; bird's nest debris from tree-hole in south-east face of willow tree, 9.i.1981. WALES, Dyfed, Rheidol Forest, bracken litter at edge of hemlock plantation, 26.ii.1981.

REMARKS. Although *C. juvenalis* was only found from the above localities, it occurred in large numbers within the samples.

Fig. 72. *Claveupodes juvenalis* n.sp.:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) palp, antiaxial;

(D) genital area ♂, sagittal.

Scale intervals 10μm.

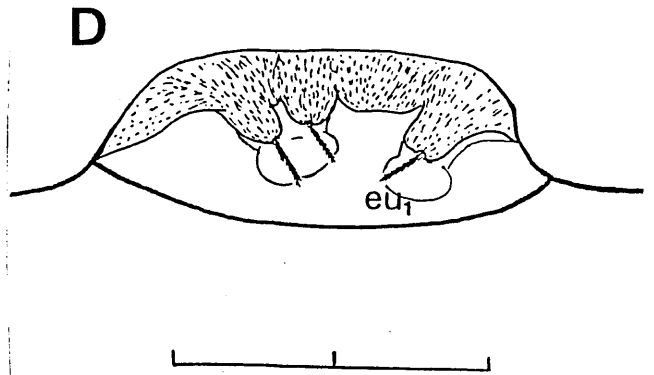
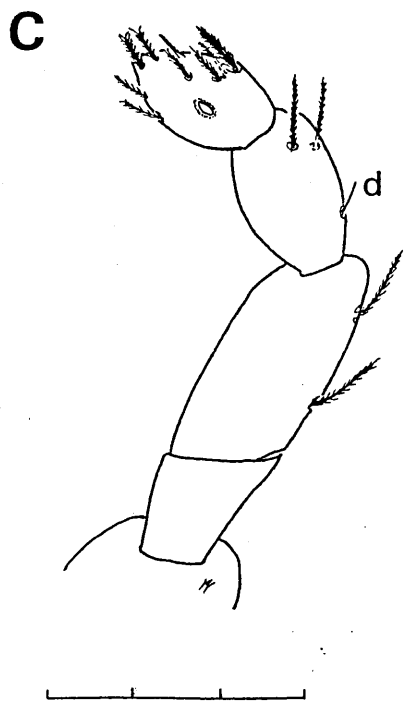
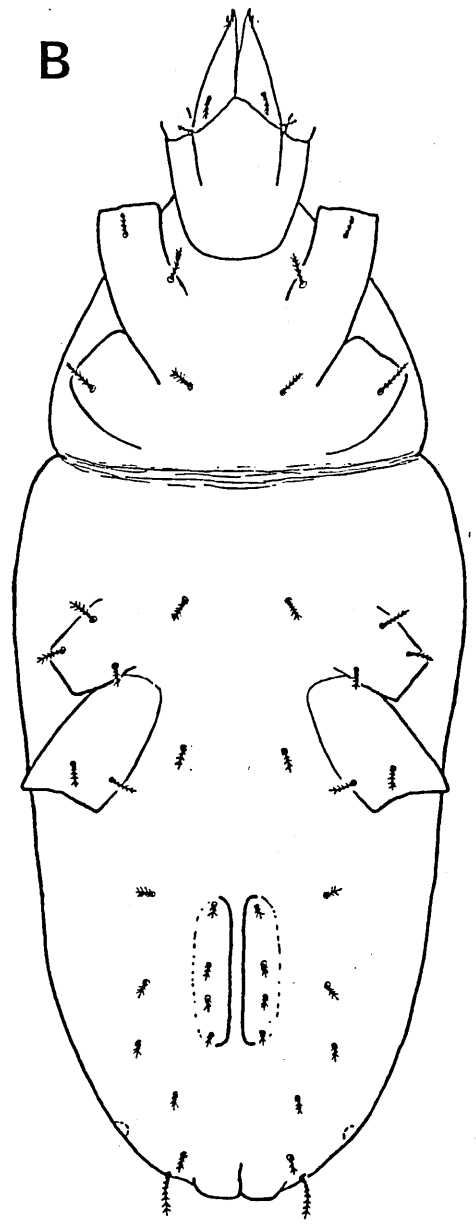
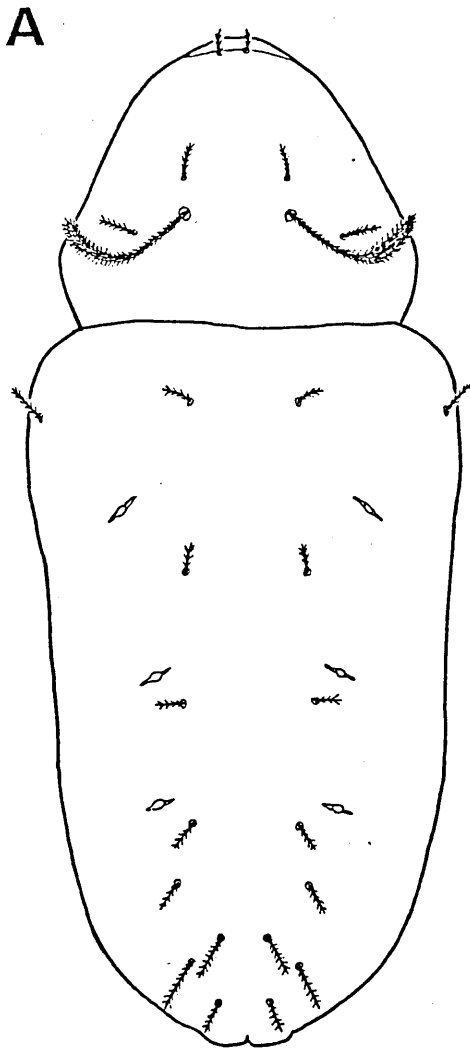
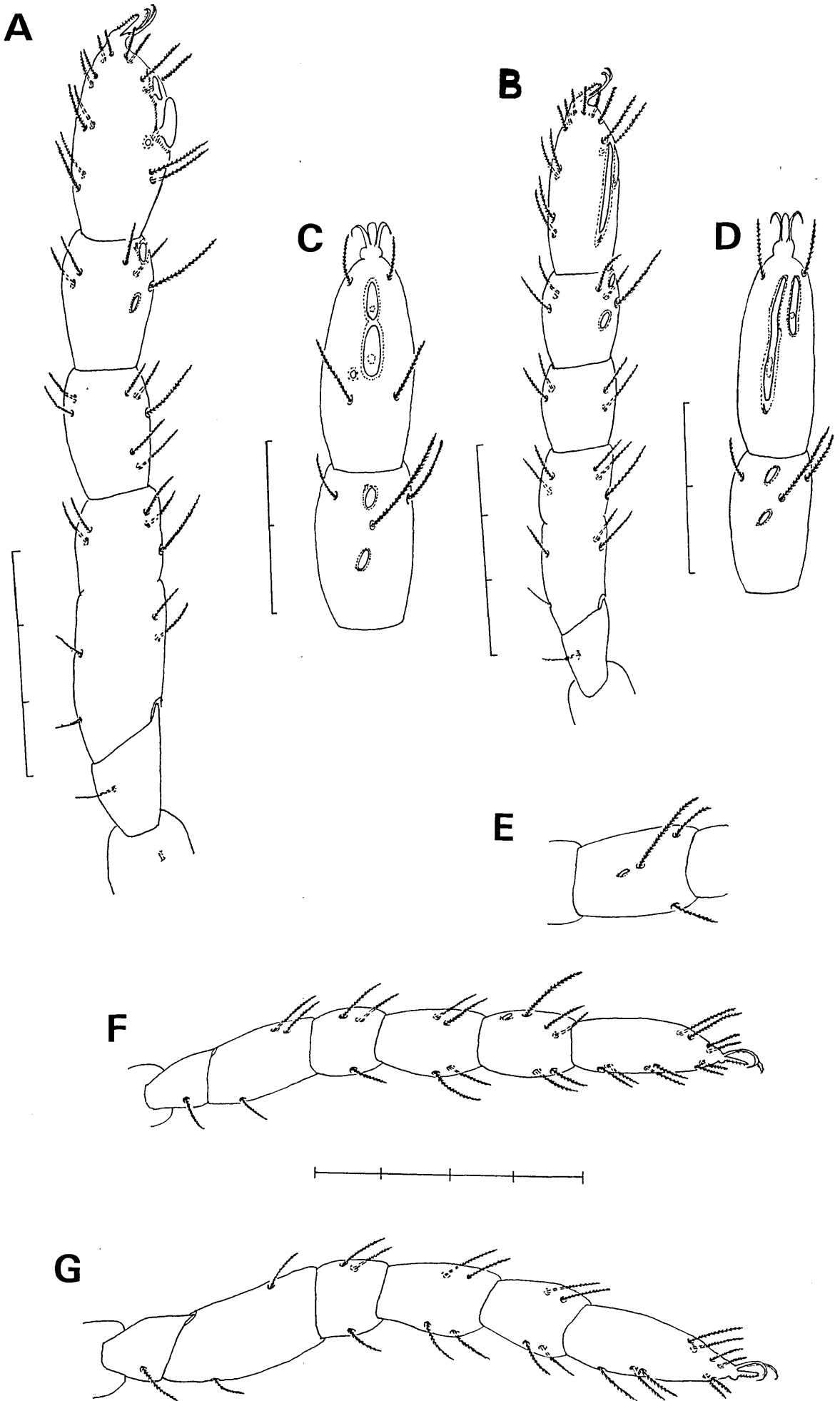


Fig. 73. *Claveupodes juvenalis* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) tibia III, dorsal;
- (F) leg III, anterolateral;
- (G) leg IV, anterolateral.

Scale intervals 10 μ m.



Clavepodes ornatus n.sp.

Figs 74 & 75

DIAGNOSIS. *C. ornatus* is immediately distinguishable from the other species of *Clavepodes* by the conspicuously papillate prodorsal shield, the heavy striations on the opisthosoma and the absence of a solenidion on tibia III.

Body length 180 (176-187), width 79 (75-83) (3 specimens examined).

GNATHOSOMA (Fig. 74B)

Subcapitulum: (*sbc*₂), ca. 6, inserted just quarter of distance from (*sbc*₁) to anterior limit of subcapitulum.

Palp: typical for genus.

Chelicera: total length 28 (26-31); *cha* 4 long.

IDIOSOMA - DORSUM (Fig. 74A)

Setae: (*iv*), (*ev*) subequal ca. 5 long; (*T*) clavate, ca. 38 long; remaining setae, subequal, ca. 10 long.

IDIOSOMA - VENTER (Fig. 74B)

Podosoma: setae - (*1c*) at 6 long approximately two-thirds length of (*1a* & *b*); remaining setae subequal, ca. 8 long.

Genital area: eugenital setae, 5 long; genital and aggenital setae subequal, ca. 8 long.

Anal region: setae subequal, ca. 12 long.

LEGS (Fig. 75).

I just below body length, II and III respectively just above and below half, IV approximately two-thirds.

Setae: formulae I 1-10(5+5)-6-5-14, II 1-10(5+5)-4-5-11,
III 1-6(2+4)-4-5-8, IV 1-5(2+3)-4-4-7.

Solenidia & famuli: rhagidial organs of tarsus I markedly enlarged, in tandem in confluent pits, occupy distal half of segment; those of tarsus II staggered parallel.

HALE. Unknown.

ETYMOLOGY. The specific name refers to the conspicuous ornamentation of the integument.

DISTRIBUTION. England.

MATERIAL EXAMINED. Holotype ♀, ENGLAND, Suffolk, Hollesley Common, from rotten pine stump, 7.iii.1964 (P.N. & K. Lawrence) [BMNH, reg.no. 1987.3.24.11]. Paratypes 2♀♀, same data as holotype [BMNH, reg.nos 1987.3.24.12-13].

REMARKS. *C. ornatus* is a rare species found only from the type locality.

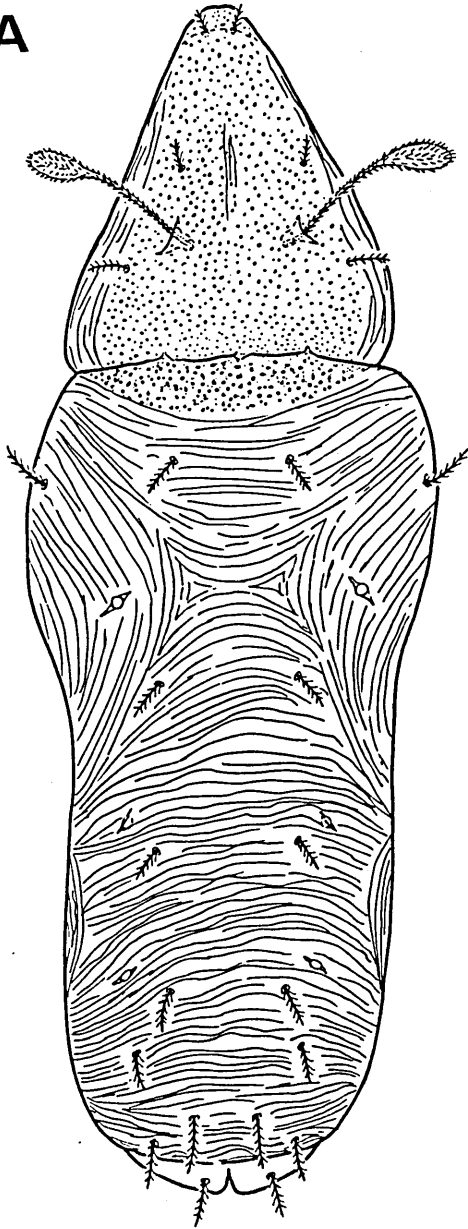
Fig. 74. *Claveupodes ornatus* n.sp.:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

Scale intervals 10 μ m.

A



B

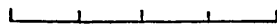
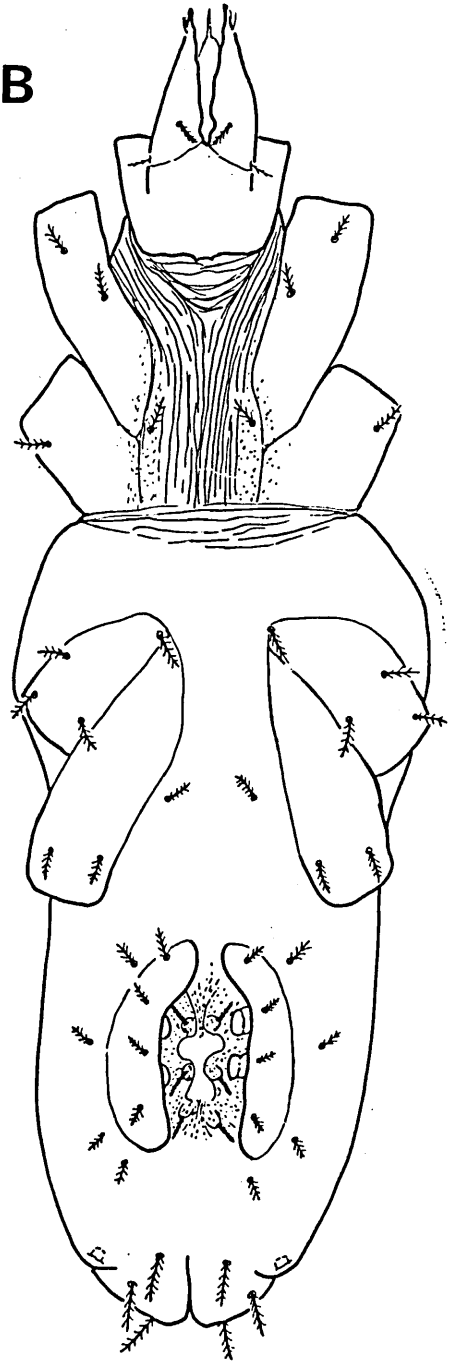
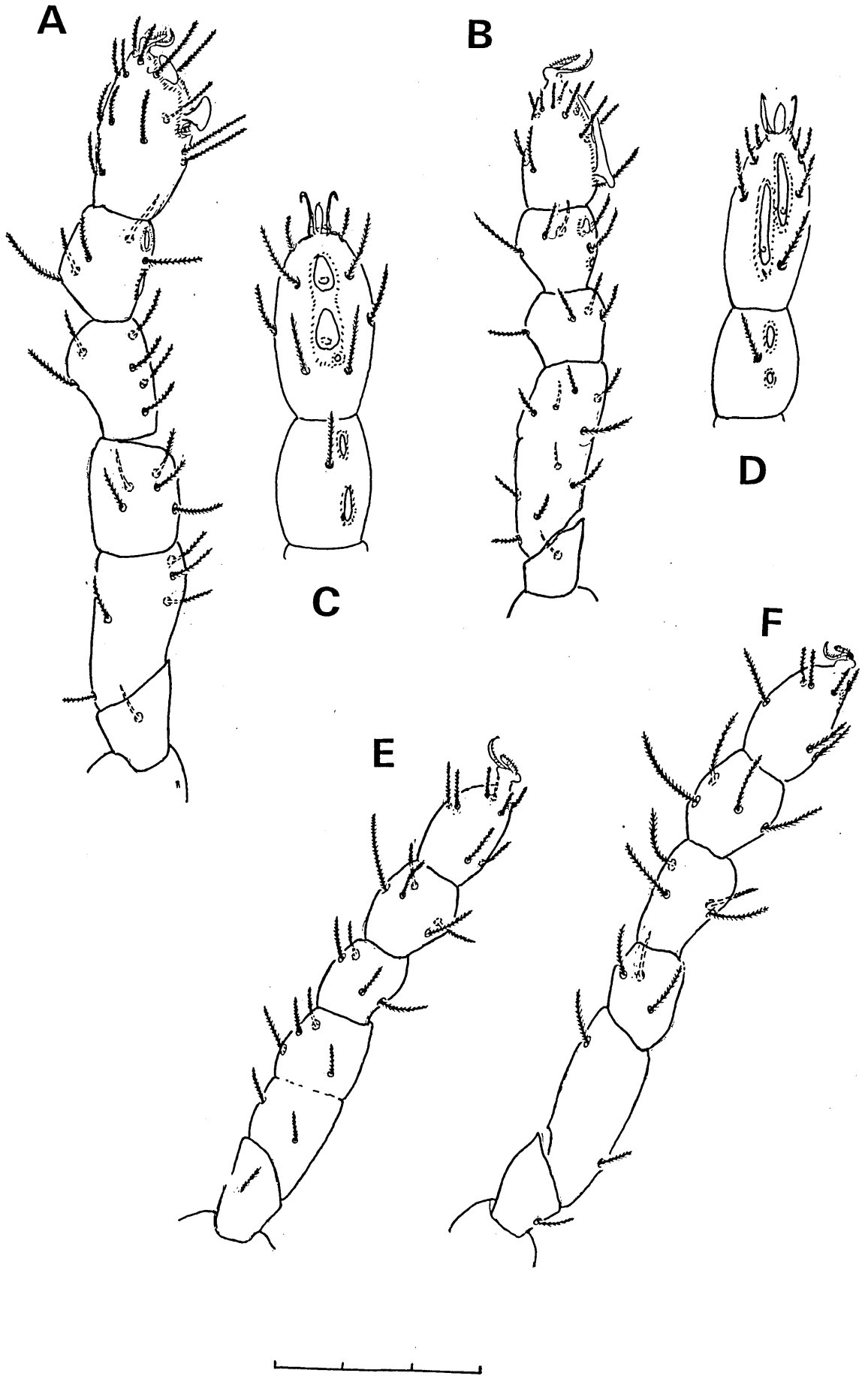


Fig. 75. *Claveupodes ornatus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.1.7 Genus *Cocceupodes* Thor

Cocceupodes Thor, 1934b: 348. Thor & Willmann, 1941: 34. Strandtmann, 1971: 85.

DIAGNOSIS. Can immediately be distinguished from other eupodid genera by the internal vertical setae being inserted posteriorly to the naso.

DEFINITION.

Small (190-450).

Integument: idiosoma weakly striate-spiculate, prodorsal shield with more densely spiculated striae; appendages spiculated.

Idiosomal form: inverted pear-shape, lateral elements of opisthosomal segment C extend anteriorly round prodorsum.

GNATHOSOMA.

Subcapitulum: ratio length to width *ca.* 1:0.6; (*sbc*₂) located approximately quarter of distance from (*sbc*₁) to anterior limit of subcapitulum.

Palp with ovoid tibiotarsus, length approximately twice the widest part; supracoxal seta terminates in crown of blunt spicules.

Chelicera: chela account for approximately one-fifth of total length; fixed digit blunt, movable digit robust in proximal half, tapers suddenly to slender point; *cha* spinose.

IDIOSOMA - DORSUM

Seiugal furrow indistinct, represented by a narrow band of striae.

Naso ranges from short extension of prodorsum to distinct lobe, without delimiting dorsal suture.

Setae: (*iv*) inserted posteriorly to *naso*, simple to capitate; (*ev*) located approximately two-thirds distance from (*T*) to anterior limit of prodorsum; (*sc*) located just anteriorly and laterally to (*T*), at widest part of body; (*c₂*) inserted markedly anteriorly to (*c₁*), approximately level with (*T*); (*c₂*), (*f₁*) and (*h₁*) often noticeably longer than other setae; (*T*) filiform, spiculated, markedly so in distal two-thirds; other setae spinose, simple, short to moderately long.

Lyrifissures: circular.

IDIOSOMA - DORSUM

Podosoma: setal formula 3-1-3-3; setae simple, spinose.

Genital area with three, four or six pairs of eugenital and genital setae, latter in single file, three or four pairs of aggenitals; eugenital setae tapering, densely spinose; genital and aggenitals simple, spinose.

Anal region: anus subterminal; two pairs pseudanal setae; (*ps₃*) markedly shorter than (*ps₁*); (*ih*) located approximately midway between (*ps₃*) and most posterior pair of aggenital setae.

LEGS.

Slender, apart from moderately to greatly enlarged femora IV; leg I usually longer than body.

Setae spinose.

Solenidia & famuli: rhagidial organs T-shaped; tarsi I and II with respectively two and three rhagidial organs, arranged in tandem and in confluent pits or staggered and parallel and in separate pits, famuli variously located; tibiae I and II with two rhagidial organs, those of I in tandem but separate pits or staggered parallel in distal half of segment, distal with famulus in same pit; organs of II proximal and distal; tibiae III and IV sometimes with one rhagidial organ.

Apotela: I reduced, usually markedly so and comprising two short hooks flanking a slightly shorter, pad-like empodium.

MALE. Sperm sac clavate, ornamented.

TYPE SPECIES. *Eupodes clavifrons* Canestrini *sp.inq.*

DISTRIBUTION. Cosmopolitan.

REMARKS. I consider the type species of *Cocceupodes* to be a *species inquirenda* since the description of *E. clavifrons* (Canestrini 1886) could now apply to more than one species. Canestrini's figure of the species, however, clearly shows the internal vertical setae to be located posteriorly to the naso and consequently there seems no doubt that the current concept of *Cocceupodes* conforms to that intended by Thor (1934).

In his description of *C. communis*, Shiba (1969) states that there are only two rhagidial organs on tarsus II instead of the normal complement of three. This feature has been repeated in taxonomic discussions (Strandtmann & Prasse 1976) but, in fact, Shiba himself corrected the number to three in his subsequent redescription (Shiba 1971).

Four species of *Cocceupodes* appear in the literature describing the British acarine fauna (Hull 1918, Turk 1953, Wood 1967). Two of these, *C. paradoxus* and *C. setosus*, were also collected during the course of the present study but I consider both of the others, *C. curviclava* Thor and *C. clavifrons*, to be *species inquirendae*. Strandtmann & Prasse (1976), in fact, synonymized these two species plus *C. australis* Strandtmann & Tilbrook with *C. mollicellus* (Koch) on the basis of similar body size, a

disregard for differences in the shape of the expanded internal vertical setae and on the assumption that the same number of genital setae occur. As will be seen from the following account of British *Cocceupodes* species, *C. minutus* n.sp., *C. australis* and *C. stellatus* would all comply with Strandtmann & Prasse's concept of *C. mollicellus* but since they differ in idiodorsal setal length, genital setal complement and leg chaetotaxy, I regard Strandtmann & Prasse's synonymies to be doubtful.

The members of *Cocceupodes* are a relatively heterogeneous group, differing in a number of features which were observed to be constant in others. Most conspicuous is the form of the internal vertical setae, which can be filiform, subclavate, clavate or capitate, and the setal complement of the genital area. In addition, the arrangement of the rhagidial organs and position of the famuli are more variable than usual. Since the different states of these characters are not congruent and so dividing the species would result in several small groupings, the genus was kept intact.

Cocceupodes shows a close affinity with *Linopodes* by sharing many features such as body form, solenidiotaxy and setal complement of coxa III and the pseudanal segment.

Key to the British species of *Cocceupodes*

- | | | |
|----|--|-------------------------|
| 1. | (iv) filiform | 2 |
| - | (iv) expanded (subclavate, clavate, capitate) | 3 |
| 2. | 6 pairs eugenital and genital setae | 4 |
| - | 4 pairs eugenital and 3 pairs genital setae | <i>C. trisetatus</i> |
| 3. | 4 pairs genital setae | 5 |
| - | 3 or 6 pairs genital setae | 6 |
| 4. | large, over 350 long; idiodorsal setae longer than intersetal distance | <i>C. setosus</i> |
| - | small, below 250 long; idiodorsal setae about half intersetal distance | <i>C. paradoxus</i> |
| 5. | large, over 350 long; idiodorsal setae longer than intersetal distance | <i>C. breweri</i> |
| - | small, below 300 long, idiodorsal setae about half intersetal distance | <i>C. australis</i> |
| 6. | (iv) subclavate; 3 pairs genital setae | <i>C. minutus n.sp.</i> |
| - | (iv) capitate; 6 pairs genital setae | <i>C. stellatus</i> |

Cocceupodes australis Strandtmann & Tilbrook

Figs 76 & 77

Cocceupodes australis Strandtmann & Tilbrook, 1968: 51.[*C. mallicellus*: Strandtmann & Prasse, 1976: 8. Misidentification]New British record

DIAGNOSIS. *C. australis* can be distinguished from other members of the genus by the clavate internal vertical setae, tarsal rhagidial organs in tandem and confluent pits and by the absence of a rhagidial organ on tibiae III and IV.

Body length 271 (244-306), width 166 (169-188).

GNATHOSOMA. (Figs 76C,D,E)Subcapitulum: subcapitular setae ca. 10 long.Palp: typical for genus.Chelicera: total length 63 (62-66); *cha* 6.**IDIOSOMA - DORSUM** (Fig. 76A)Naso: rounded triangular.

Setae: (*iv*) clavate with distinct pedicel; moderately short, extending only about halfway to base of seta following; lengths - (*iv*) 25 (23-28), (*ev*) 19 (17-20), (*T*) 65 (59-70), (*sc*) 20 (18-21), (*c*₁) 22 (20-23), (*c*₂) 44 (42-47), (*d*₁) 22 (20-24), (*e*₁) 23 (20-25), (*f*₁) 29 (27-30), (*f*₂) 25 (23-27), (*h*₁) 33 (28-37), (*h*₂) 24 (20-29).

IDIOSOMA - VENTER (Figs 76B,F)

Podosoma: (*1c*) 8 long, approximately third length of (*1a* & *b*), (*2b*) 25 (22-27), (*3a*) approximately three-quarters length of (*2b* & *c*), ca. 20 long, (*4a*) 11, approximately two-thirds length of (*4b* & *c*).

Genital area: three pairs eugenital setae, ca. 6 long, eu_2 , eu_3 , eu_4 grouped slightly apart from eu_1 ; four pairs subequal, 7 long, genital setae; three pairs aggenitals, decrease gradually in length posteriorly from 9 to 5; three gravid specimens, each with a single ovoid egg, ca. 100 by 75.

Anal region: (ps_1) 30 (27-32), approximately four times (ps_3).

LEGS (Fig. 77)

I 1.2 times body length, II two-thirds times, III slightly longer than II, IV just shorter than body; femur IV greatly enlarged.

Setae: formulae I 1-14 (9+5)-7-11-19; II 1-11 (6+5)-4-6-13;

III 1-7 (3+4)-4-5-14; IV 1-6 (3+3)-4-5-13.

Solenidia & famuli: tarsal rhagidial organs in tandem and confluent pits; those of tibia I in tandem; otherwise typical for genus.

Apotela: I reduced, half size of apotele II.

MALE. Unknown.

DISTRIBUTION. South Atlantic Islands (Signy, South Orkney Islands; Deception, South Shetland Islands), Eire, England, Scotland, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, DECEPTION ISLAND, moss, 20.i.1964 (P J Tilbrook). Paratypes 7 ♀♀, same data as holotype.

British material: ENGLAND, Devon, near Cornwood, Dartmoor, Higher Piles Copse (oak wood), from moss mat, mostly *Hypnum cupressiforme*, from surface of jumbled boulders in wood, 3.vi.1934 (P D Hillyard).

OTHER BRITISH RECORDS. EIRE, Galway, from moss, turf & lichens by bog, 20.viii.1981 (K. P. Martyn). ENGLAND, Suffolk, Hollesley Common, from

rotten pine stump, 7.iii.1964 (P N & K Lawrence); Yorkshire, Ilkley Moor, near Cow & Calf rocks, from *Polytrichum* moss covering stones amongst heather, 20.ii.1982. SCOTLAND, Strathclyde, western shore of Loch Lomond, by Endrich Water, from litter in hole in willow trunk at ground level, 12.ix.1982; Strathclyde, Inchcailloch (main island in Loch Lomond), area of understory ferns, from litter and fermentation layers under oak, 13.ix.1982

REMARKS. (See also generic REMARKS) Shiba (1971) synonymized the species *C. communis* Shiba with *C. australis*, the latter taking priority. Strandtmann & Prasse (1976), however, expressed doubt about the validity of this action, a view which I support. Shiba's decision, based on comparison of the descriptions and not of the type material, allowed for variation in genital setation, a feature shown in this study to be constant, at least at specific level. Other differences occur in the size ranges and position of the internal vertical setae and further indicate that the synonymy is incorrect.

C. australis is most similar to *C. breweri*; both possess the same form of internal vertical setae, arrangement of rhagidial organs and complement of genital setae. *C. australis*, however, differs by its smaller size, shorter setae, the absence of a rhagidial organ on tibiae III and IV and by the leg chaetotaxy.

C. australis was the most commonly collected species of the genus, being found in most samples of litter, moss and grassland.

Fig. 76. *Cocceupodes australis*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial;
- (F) genital area ♀, sagittal.

Scale intervals 10µm.

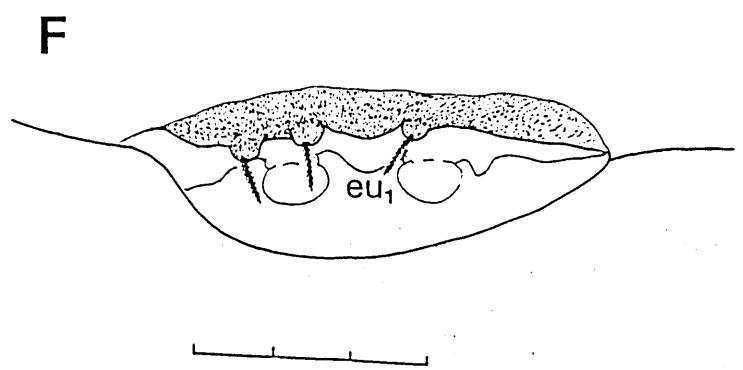
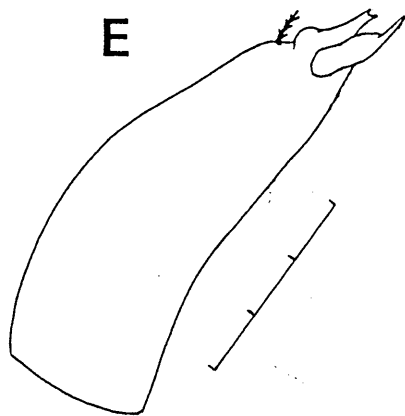
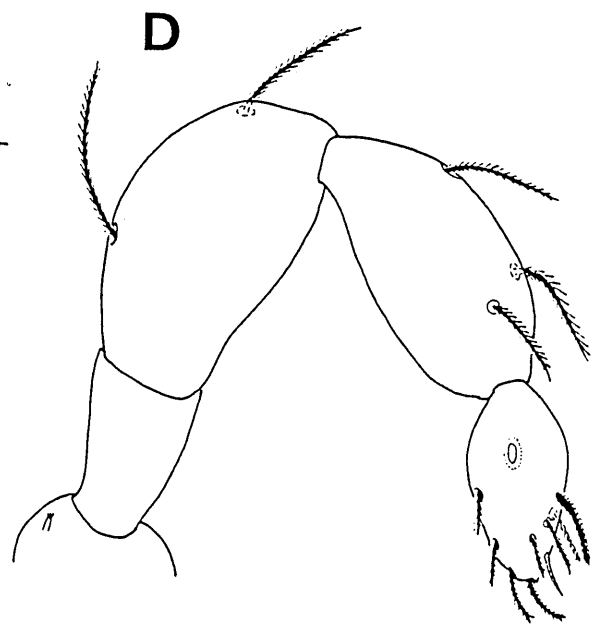
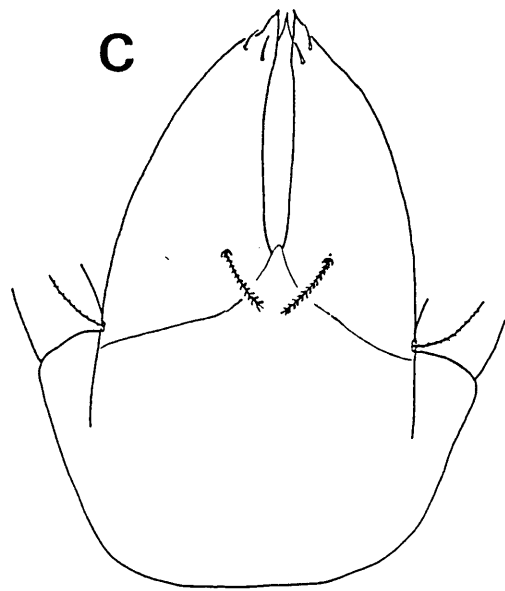
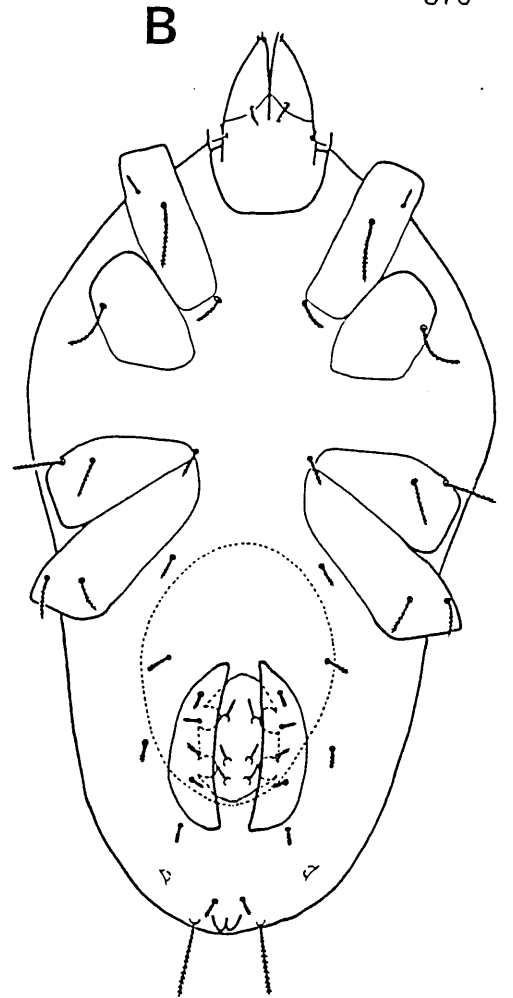
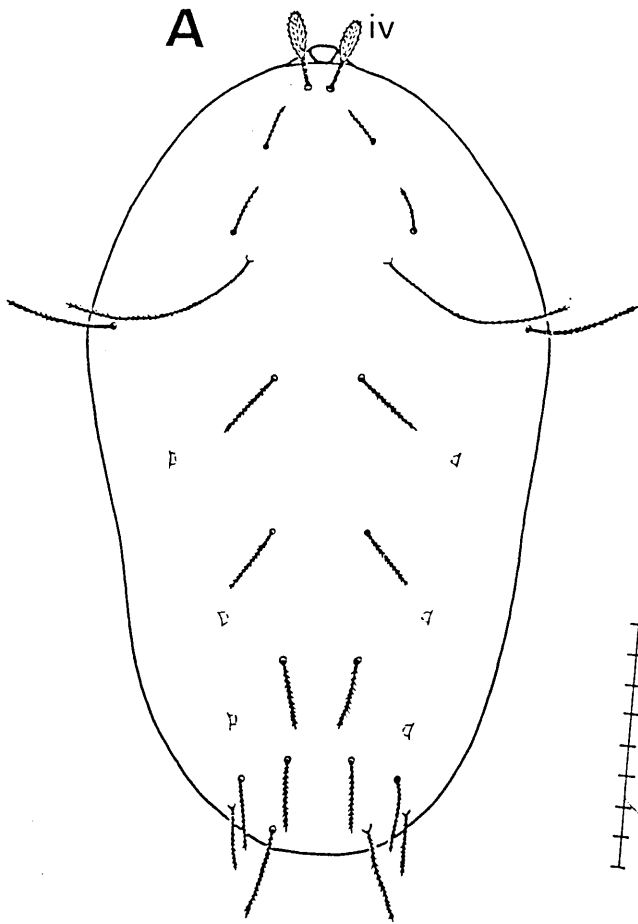
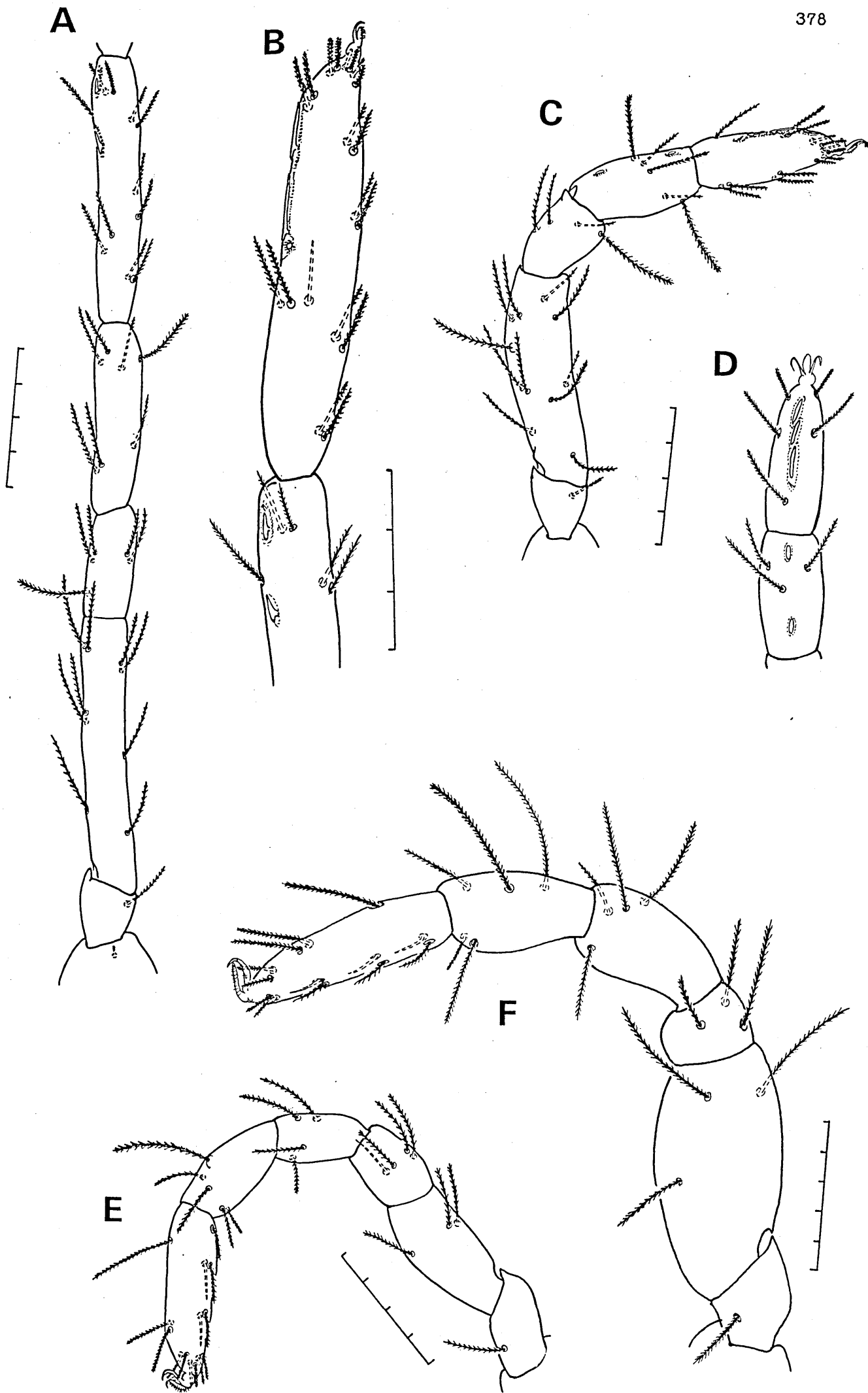


Fig. 77. *Cocceupodes australis*:

- (A) trochanter to tibia I, posterolateral;
- (B) tarsus I & distal portion of tibia I, posterolateral;
- (C) leg II, posterolateral;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Cocceupodes breweri Strandtmann

Figs 15f, 17c, 20d,f, 78 & 79

Cocceupodes breweri Strandtmann, 1971: 87.New British record

DIAGNOSIS. Can be distinguished from the other members of the genus by the combination of clavate internal vertical setae, idiodorsal setae which are longer than intersetal distances and four pairs of genital setae.

Body length 350 (331-398), width 203 (197-214).

GNATHOSOMA (Figs 15f, 17c, 78B)

Subcapitulum: subcapitular setae ca. 10 long.

Palp: typical for genus.

Chelicera: total length 57 (53-62); *cha* ca. 6 long.

IDIOSOMA - DORSUM (Figs 20d,f, 78A)

Naso: distinct, rounded triangular lobe.

Setae: (*iv*) clavate, inserted just posterior to base of naso; long, reaching base of seta following, lengths - (*iv*) 47 (44-52), (*ev*) 50 (47-52), (*T*) 118 (115-123), (*sc*) 42 (39-44), (*c₁*) 85 (81-88), (*c₂*) 62 (57-66), (*d₁*) 78 (74-84), (*e₁*) 79 (74-83), (*f₁*) 70 (67-73), (*f₂*) 57 (54-60), (*h₁*) 73 (68-76), (*h₂*) 49 (45-53).

IDIOSOMA - VENTER (Fig. 78B)

Podosoma: (*1c*) ca. 10 long, respectively third and two-thirds length of (*1a*) and (*1b*); remaining setae 30-35 long.

Genital area: three pairs short, ca. 4, eugenital setae; four pairs genital and aggenital setae; (g_1) at ca. 12 noticeably longer than remainder.

Anal region: (ps_1), at ca. 23 long, approximately three times (ps_3).

LEGS (Fig. 79)

I 1.5 times body length, II and III respectively just below and above two-thirds, IV just below body length.

Setae: formulae I 1-14(9+5)-8-11-20, II 1-11(6+5)-4-6-13,

III 1-7(3+4)-4-5-13, IV 1-6(3+3)-4-5-13.

Solenidia & famuli: tarsi I and II with rhagidial organs lying in tandem in confluent pits, famuli in same pit as organs; rhagidial organs of tibiae I in tandem but separate pits; dorsomedian rhagidial organ present on tibiae III and IV.

MALE. (Fig. 78C) (3 specimens examined). Sperm sac clavate, unornamented although with granular appearance.

DISTRIBUTION. England, Alaska, Scotland, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, ALASKA, Anaktuvik Pass, from tundra samples, 17.vi.1968 (K. & D. Pittard) IBM, slide no. 93431.

British material: ENGLAND, Suffolk, Hollesley Common, from pine litter, 24.ii.1984; Wiltshire, Savernake Forest, birch copse in eastern part of forest, with patches of understorey brambles, from moss round base of birch plus 0.5cm of underlying soil, 17.ix.1981.

OTHER BRITISH RECORDS. ENGLAND, Devon, Braunton Burrows, slacks between mature dunes, from moss by clump of *Carex* plus 3cm of underlying sandy soil, 7.xii.1981; Kent, Canterbury Nature Reserve, grassy bank near power

substation, from *Deschampsia/Agrostis* spp. plus 2cm of underlying clay soil, 17.iii.1981; Yorkshire, Ilkley Moor, below 'Cow and Calf' rocks, from moss, lichens and *Calluna* roots growing over stones, 20.22.81; Surrey, Chobham Common, from moss and lichens under birch bush, 19.v.1982.

SCOTLAND, Sutherland, Torboll, near Golspie, ca. sea level, from alder carr grass and leaf litter, 29.vi.1976 (P. D. Hillyard); Tayside, Rannoch Forest, from litter and fermentation layers under spruce at edge of forest, 15.ix.1982. WALES, Dyfed, near Tregaron, Cors Tregaron, West bog, raised *Sphagnum* bog, from layer of *Eurynchium* moss under *Calluna*, 24.ii.1981.

Fig. 78. *Cocceupodes breweri*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

Scale intervals 10 μ m.

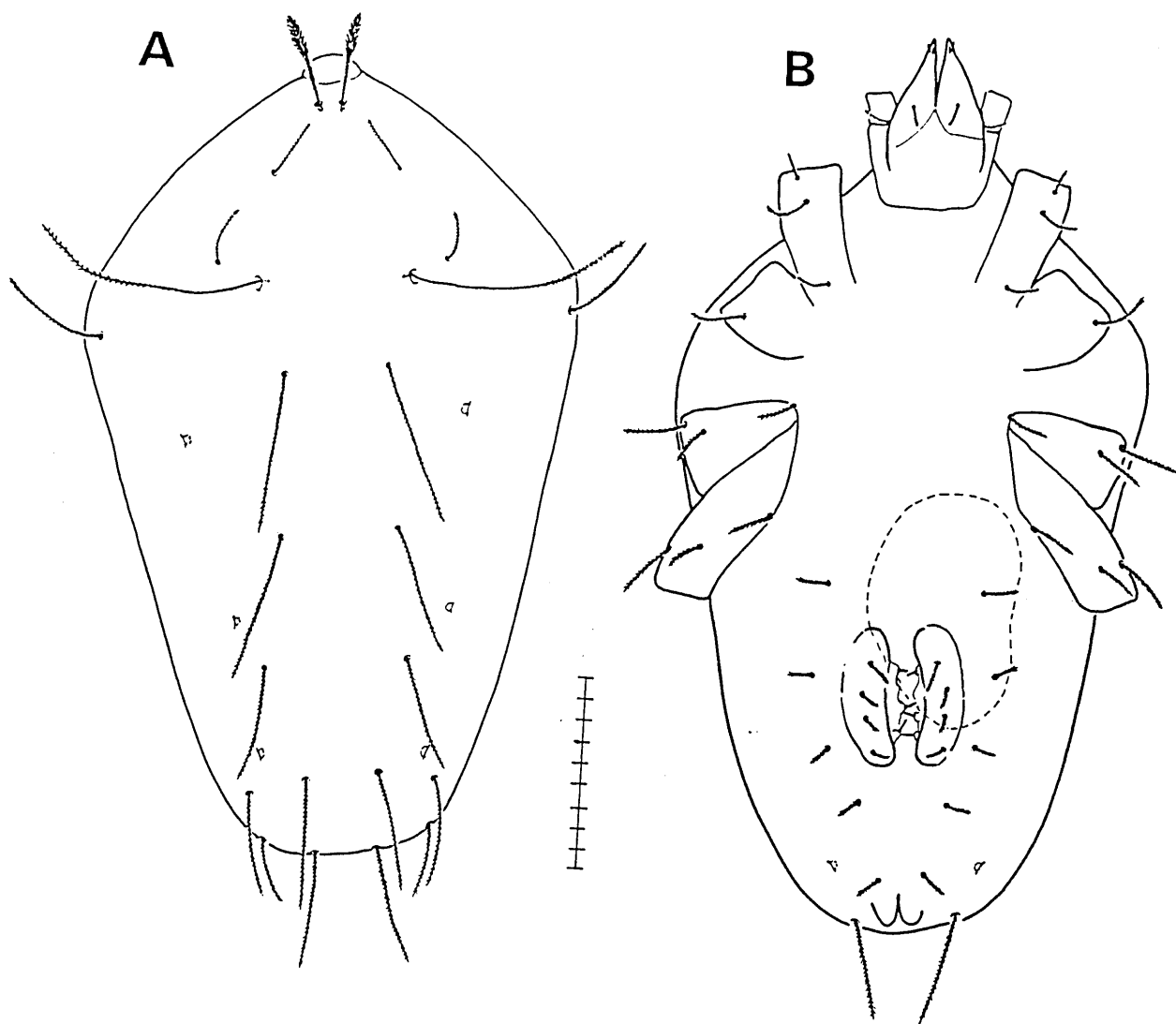
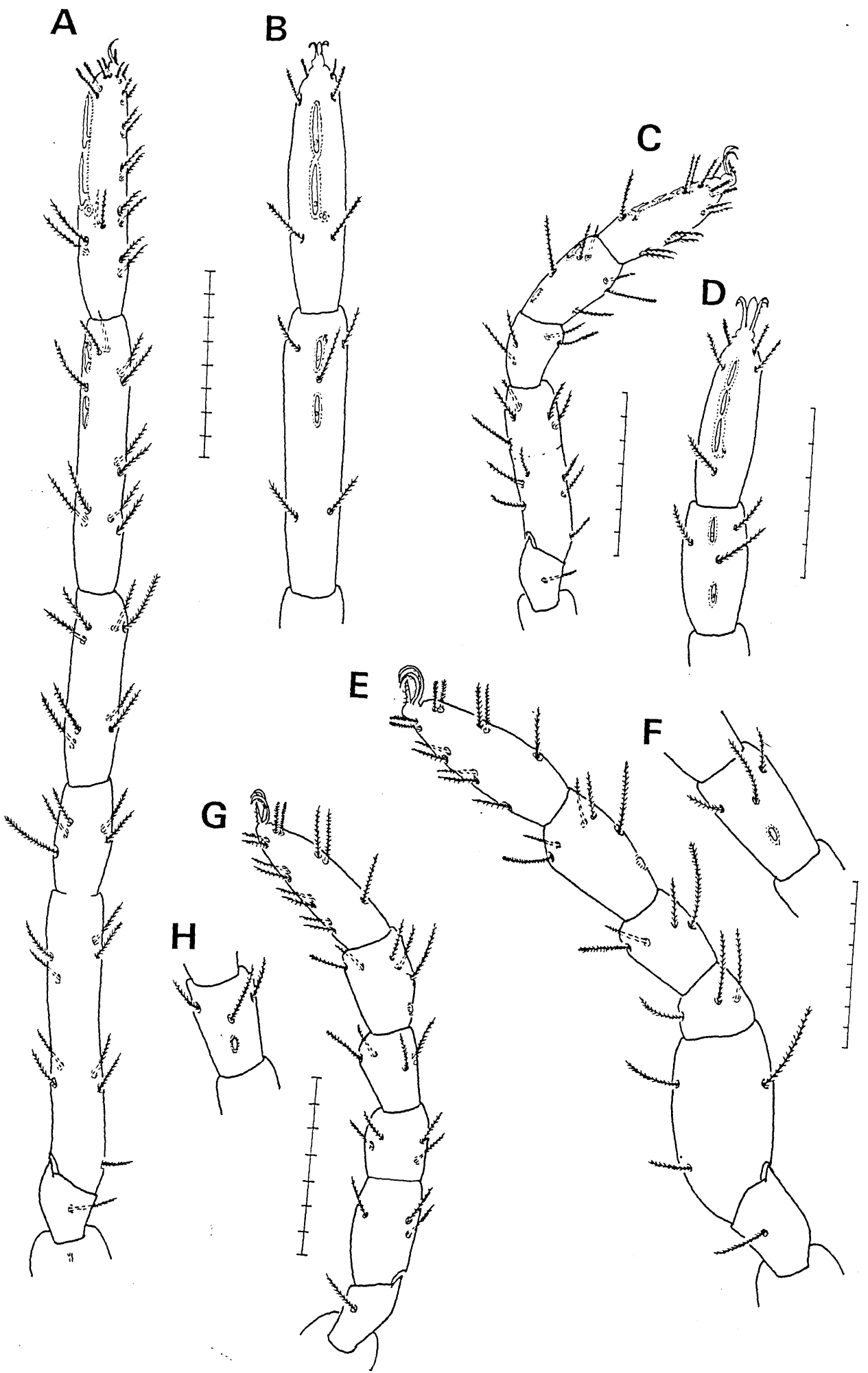


Fig. 79. *Cocceupodes breweri*:

- (A) leg I, posterolateral;
- (B) tarsus & tibia I, dorsal;
- (C) leg II, posterolateral;
- (D) tarsus & tibia II, dorsal;
- (E) leg IV, anterolateral;
- (F) genu IV, dorsal;
- (G) leg III, anterolateral;
- (H) genu III, dorsal.

Scale intervals 10 μ m.



Cocceupodes minutus n.sp.

Figs 80 & 81

DIAGNOSIS. This species can be distinguished from other members of the genus *Cocceupodes* by its small size, the subclavate internal vertical setae and the presence of only three pairs of genital setae.

Body length 203 (194-221), width 97 (90-107).

GNATHOSOMA (Fig. 80B)

Subcapitulum: subcapitular setae ca. 8 long.

Palp: typical for genus.

Chelicera: total length 43 (40-45); *cha* 5 long.

IDIOSOMA - DORSUM (Fig. 80A)

Naso: small peak.

Setae: (*iv*) subclavate; generally short, extending approximately third distance to seta following, lengths - subequal ca 13-15, apart from (*T*), 47 (44-49) and subequal (*c*₂), (*h*₁)), (*f*₁) 21-24.

IDIOSOMA - VENTER (Fig. 80B)

Podosoma: (*1c*) at 5 long, approximately one third length of (*1b* & *c*), (*2b*) at 22, rather longer than others, (*3a*) 8, (*3b* & *c*) 12-14, (*4a-c*) increase in length gradually from 9-14.

Genital area: four pairs eugenital setae, subequal ca. 5 long; three pairs genital setae, subequal ca. 6 long; four pairs aggenital setae 8-9 long.

Anal region: (*ps*₁), at 27 (25-30), approximately three times longer than (*ps*₂).

LEGS (Fig. 81)

I approximately body length, II and III respectively just above and below half body length, IV approximately three-quarters body length.

Setae: formulae I 1-12(7+5)-6-9-18, II 1-10(5+5)-4-5-13,
III 1-7(3+4)-4-5-13, IV 1-6(3+3)-4-5-12.

Solenidia & famuli: rhagidial organs of tarsus I staggered, parallel, in separate pits; those of II in N-shaped arrangement, famulus not discerned; tibiae III and IV with one rhagidial organ dorsomedially.

Apotele: I reduced, approximately half size of II.

MALE. Unknown.

ETYMOLOGY. The specific name refers to the size of this species which is, to date, the smallest member of the genus.

DISTRIBUTION. England, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, ENGLAND, Cornwall, Goonhilly Downs, from moss mat covering rocks amongst heather, 8.xii.1981 [BMNH, reg. no. 1987.3.24.14]. Paratypes: 5 ♀♀, same data as holotype; 4 ♀♀, same locality as holotype, from aerial parts of *Calluna* plus 2cm of underlying roots and soil, 8.xii.1981 [BMNH, reg. nos 1987.3.24.15-23].

OTHER BRITISH RECORDS. ENGLAND, Berkshire, Windsor Forest, from litter inside hollow aged oak tree, 4.i.1976 (P. D. Hillyard); Cornwall, Goonhilly Downs, near Gweek, from moss off stone pillar under oak tree, 8.xii.1981; Essex, Colne Point Nature Reserve, ca. 500m south of North Mud Flats & 30m inland, along *Sueda* path, from aerial parts of sea purslane and 3cm of underlying soil, 12.5.1981; Suffolk, 1.5km SW of Walberswick, Dingle

Great Hill, from mixed grass, moss and lichen (predominantly *Agrostis*,
Cladonia, *Pleurozium schreberi*) by patch of heath, 7.i.1981. WALES, Dyfed,
Rheidol Forest, from bracken litter at edge of forest by field centre,
25.ii.1981.

REMARKS. See generic **REMARKS**.

Fig. 80. *Cocceupodes minutus* n.sp.:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area ♀, sagittal.

Scale intervals 10 μ m.

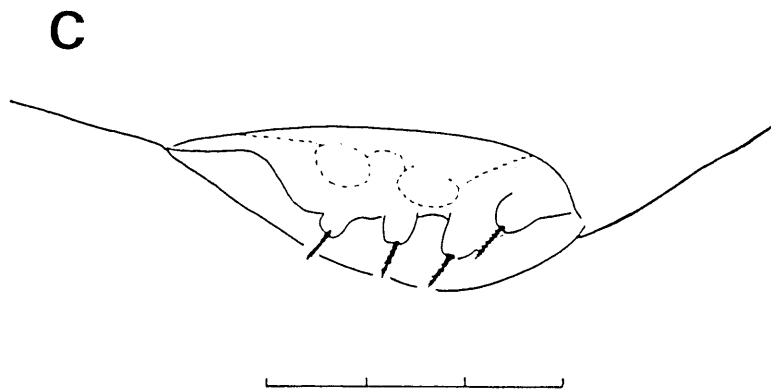
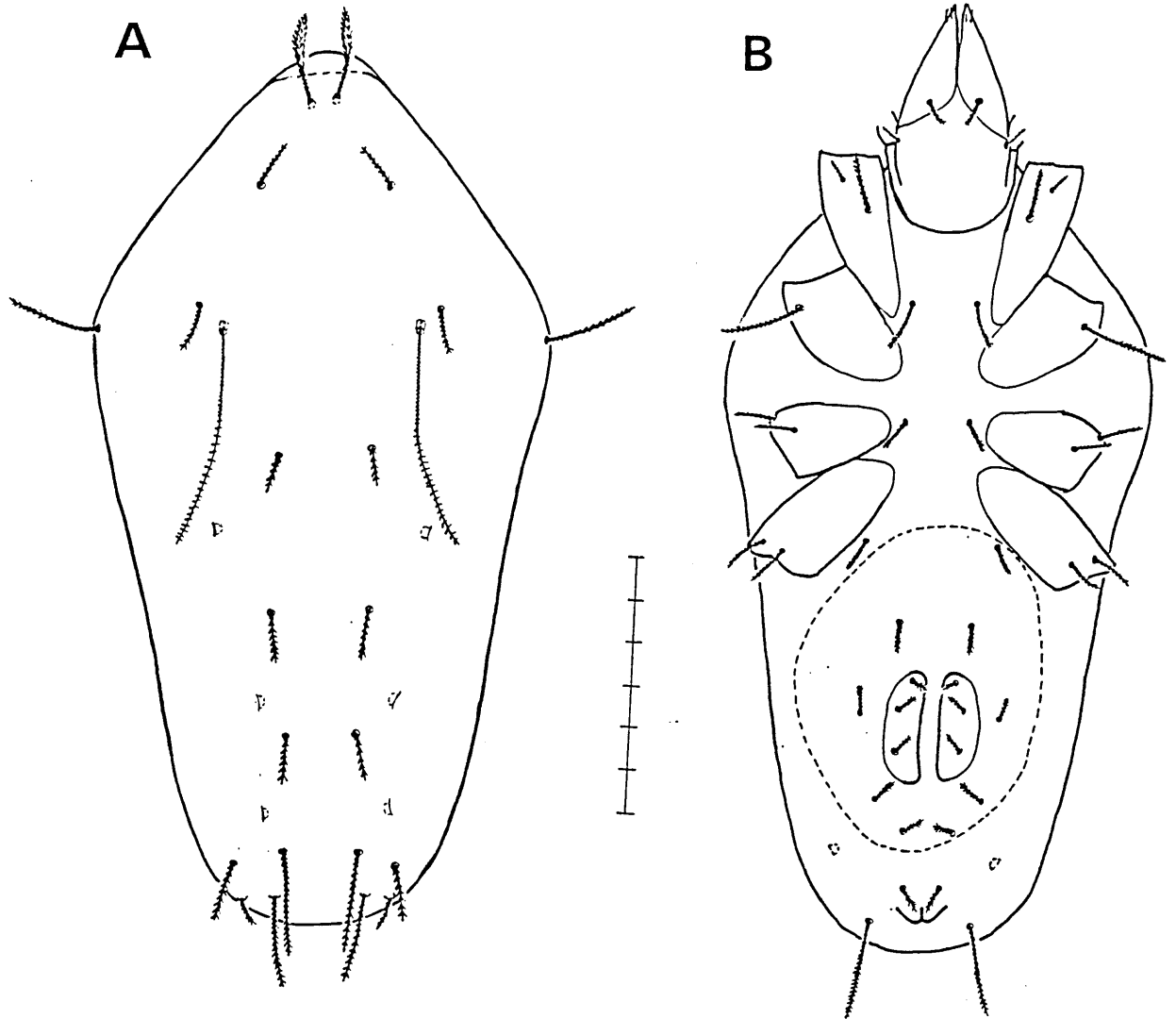
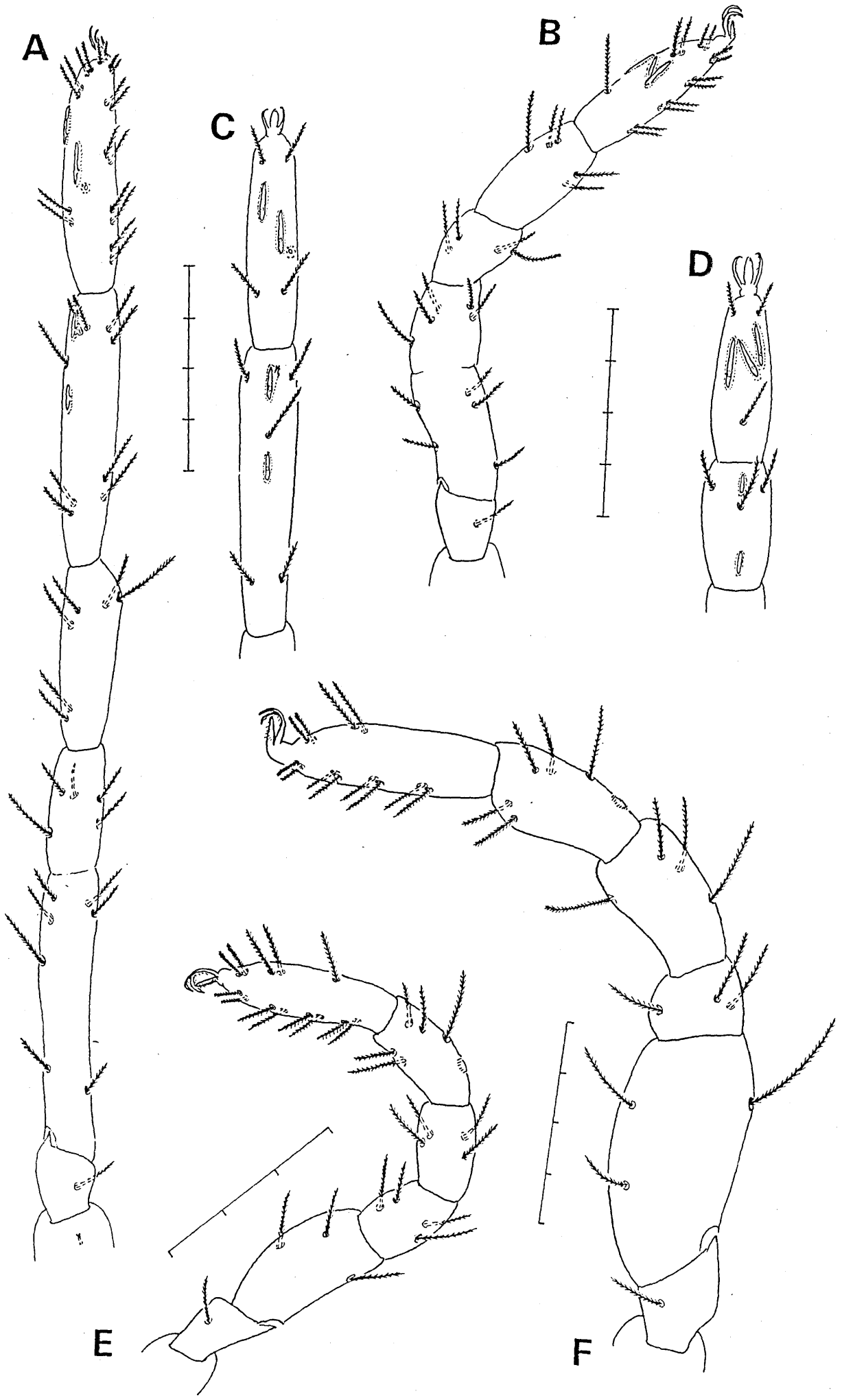


Fig. 81. *Cocceupodes minutus* n.sp.:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Cocceupodes paradoxus Weis-Fogh

Figs 82 & 83

Cocceupodes paradoxus Weis-Fogh, 1948: 263.

DIAGNOSIS. *C. paradoxus* can be distinguished from other members of the genus by the combination of simple internal vertical setae, short idiosomal setae and six pairs of genital setae.

Body length 219 (209-225), width 111 (103-116).

GNATHOSOMA (Fig. 82B)

Subcapitulum: subcapitular setae 9 long.

Palp: typical for genus.

Chelicera: total length 43 (40-45); *cha* 4 long.

IDIOSOMA - DORSUM (Fig. 82A)

Naso: roughly triangular peak.

Setae: (*iv*) simple; mostly short, lengths - (*iv*) 30 (27-32),

(*ev*) 12 (10-14), (*T*) 75 (69-81), (*sc*) 23 (19-26), (*c₂*) 48 (45-51), (*c₁*), (*d₁*),

(*e₁*), (*f₂*) and (*h₂*) subequal ca. 14-16 long, (*f₁*) 40 (37-42),

(*h₁*) 30 (28-34).

IDIOSOMA - VENTER (Figs 82B,C)

Podosoma: (*1c*) 6 long, approximately half length of (*1a & b*), (*2b*) 16 (14-17), (*3a*) at 10 approximately three-quarters length (*3b & c*), (*4a*) at 9, approximately two-thirds (*4b & c*).

Genital area: six pairs eugenital setae, ca. 4 long; six pairs subequal genital setae, 7-8 long; four pairs subequal aggenital setae, ca. 11 long.

Anal region: (*ps₁*) at ca. 13 long, approximately twice length (*ps₂*).

LEGS (Fig. 83)

I just over body length, II and III respectively just below and above two-thirds body length, IV just below body length.

Setae: formulae I 1-12(7+5)-7-9-18; II 1-11(6+5)-4-5-13;

III 1-7(3+4)-4-5-12; IV 1-7(4+3)-4-5-11.

Solenidia & famuli: rhagidial organs of tarsus and tibia I staggered parallel in separate pits, famulus located posterolaterally in separate pit; rhagidial organs of tarsus II in tandem and parallel in separate pits, famulus posterolateral to base of proximal organ; dorsoproximal rhagidial organ on tibiae III and IV.

Apotela: I not markedly reduced, about three-quarters size of II.

MALE. (Fig. 82C) (2 specimens examined) Sperm sac clavate, unornamented.

DISTRIBUTION. England, Norway, Scotland, Wales.

MATERIAL EXAMINED. ENGLAND, Surrey, Whitelands, area of chalkland, from moss, aerial parts of thyme and grass plus underlying 2cm of soil, 19.v.1982; Box Hill, Happy Valley, from surface of grassland, 2.vi.1982.

OTHER BRITISH RECORDS. ENGLAND, Staffordshire, Cannock Chase, from grass, fungus, moss and rotten wood in silver birch stump (approximately 20cm high), 19.ii.1982; Cheshire, Ellesmere Port, arable field by Sycamore Road, from moss, grass and fungi growing on uprooted oak tree, 26.ii.1982.

SCOTLAND, Strathclyde, Loch Lomond Nature Reserve, copse at edge of Twenty Acre Field, from debris and litter under hawthorn, 12.ix.1982; birch wood along western edge of Loch, from birch litter, 12.ix.1982.

WALES, Dyfed, Borth, Ynyslas Nature Reserve, from moss between mature

sand dunes, 25.ii.1981; Rheidol Forest, clearing ca. 20m from edge of forest, from bracken litter, 26.ii.1981.

REMARKS. See generic REMARKS.

Fig. 82. *Cocceupodes paradoxus*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area ♀, sagittal.

Scale intervals 10 μ m.

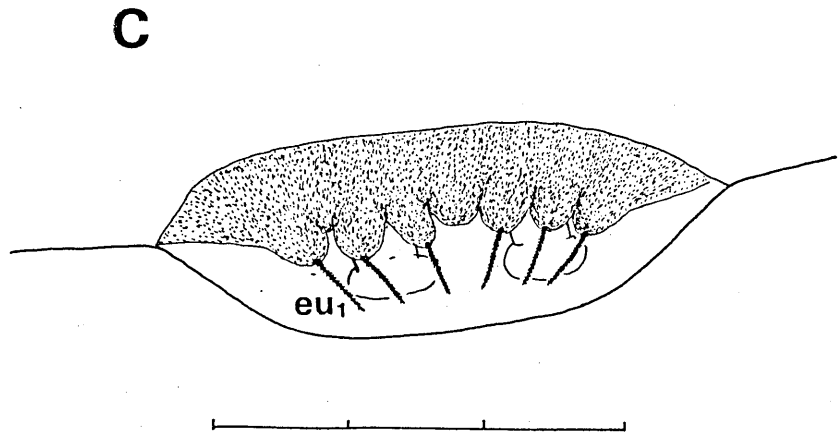
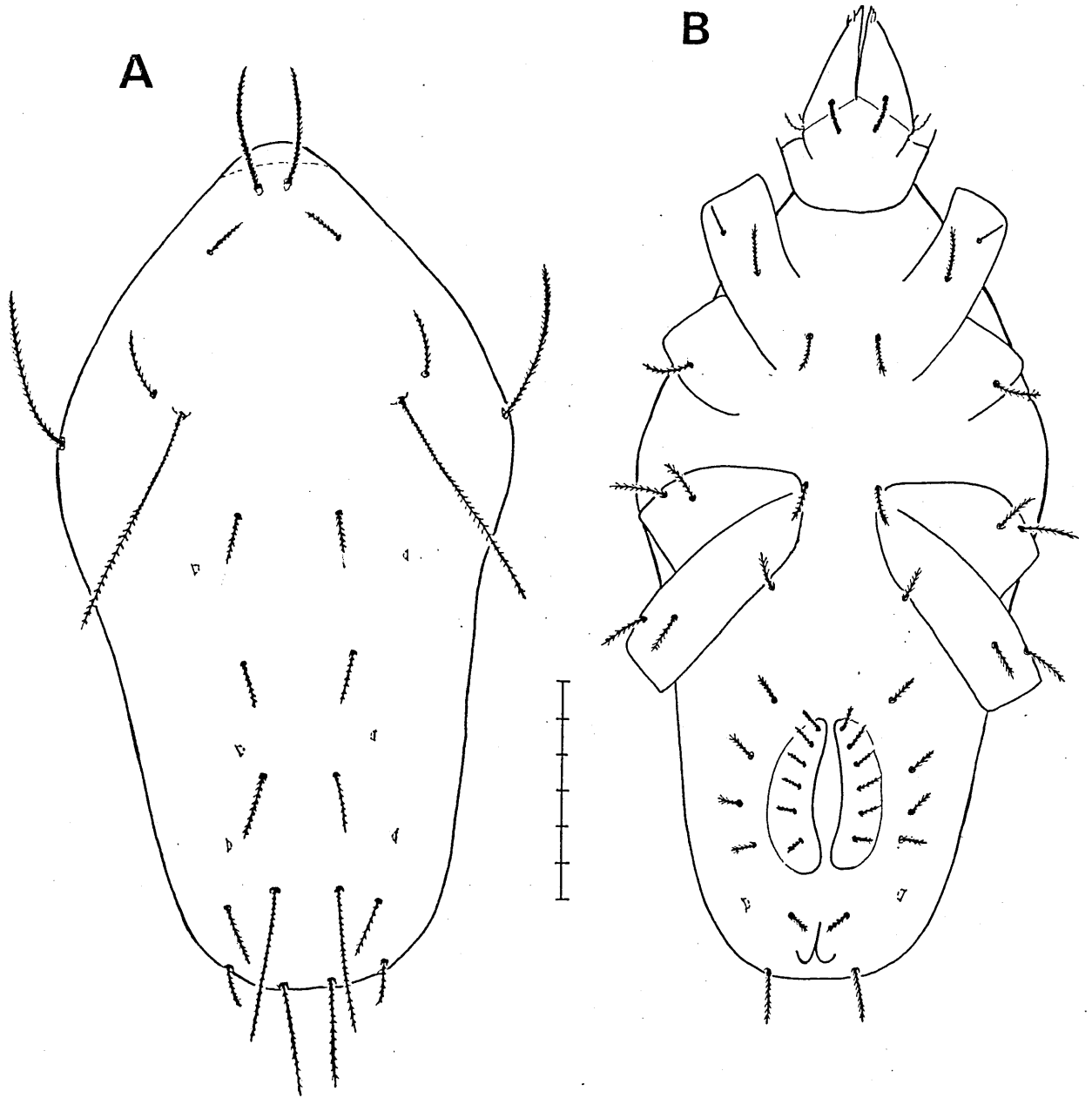
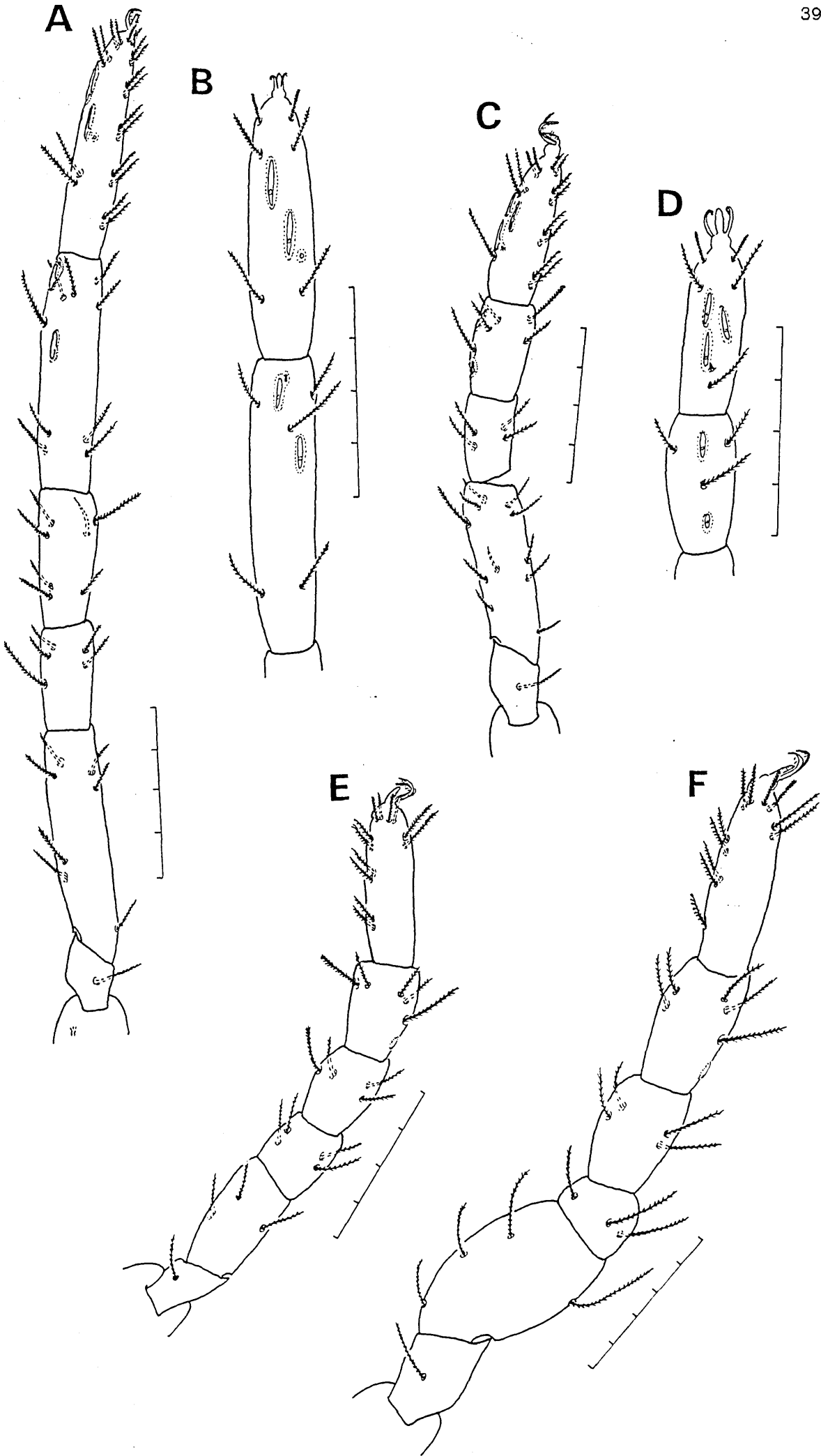


Fig. 83. *Cocceupodes paradoxus*:

- (A) leg I, posterolateral;
- (B) tarsus & tibia I, dorsal;
- (C) leg II, posterolateral;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Cocceupodes setosus Evans

Figs 84 & 85

Cocceupodes setosus Evans, 1954: 801.*Cocceupodes shepardii* Strandtmann, 1971: 88. n.syn.

DIAGNOSIS. Can be distinguished from other species of *Cocceupodes* by its relatively large size, the filiform internal vertical setae and the presence of six pairs of both eugenital and genital setae.

Body length 396 (364-417), width 152 (139-174).

GNATHOSOMA (Fig. 84B)

Subcapitulum: subcapitular setae ca. 12 long.

Palp: typical for genus.

Chelicera: total length 63 (59-68); *cha* ca. 6 long.

IDIOSOMA - DORSUM (Fig. 84A).

Naso: rounded triangular peak.

Idiosomal setae: (*iv*) simple (*ev*); all long, just overlapping base of seta following, lengths - (*iv*) 40 (36-43), (*ev*) 37 (35-41), (*T*) 87 (82-94), (*sc*) 58 (55-62), (*c*₁) 33 (30-37), (*c*₂) 60 (56-63), (*d*₁) 62 (57-65), (*e*₁) 34 (29-37), (*f*₁) 65 (61-68), (*f*₂) 31 (27-34), (*h*₁) 54 (47-56), (*h*₂) 29 (26-33).

IDIOSOMA - VENTER (Fig. 84B)

Podosoma: (*1c*) ca. 11 long, approximately one third length of subequal remainder.

Genital area: six pairs subequal eugenital setae, ca. 7 long; six pairs genital setae, subequal ca. 10 long; four pairs aggenital setae, subequal ca. 13 long.

Anal region: (ps_1) almost terminal, at ca. 26, twice length of (ps_4).

LEGS (Fig. 85)

I fifth longer than body, II and III respectively just below and above half, IV approximately three-quarters body length.

Setae: formulae I 1-12(7+5)-11-13-22, II 1-11(6+5)-4-5-16, III 1-8(4+4)-4-5-14, IV 1-7(4+3)-4-5-13.

Solenidia & famuli: tarsi I and II with rhagidial organs in tandem and confluent pits, famuli subtending; tibiae I and II with rhagidial organs in tandem but separate pits; dorsoproximal rhagidial organ on tibiae III and IV.

Apotela: I reduced, just over half size of II.

MALE. (1 specimen examined) (Fig. 84C) Sperm sac clavate, unornamented.

DISTRIBUTION. Alaska, Eire, England, Scotland, Wales.

MATERIAL EXAMINED. Type material: *C. setosus*, holotype ♀, EIRE, Co. Clare, The Burren, from moss, 6.vi.1951 (J. Duffy) [BMNH, reg. no. 1953.1.2.511]. *C. shepardi*, holotype ♀, ALASKA, Cape Beaufort, tundra (moss & prostrate birch), 17.vii.1968, (R W & M R Strandtmann) [BM, slide no. 9344]. British material: ENGLAND, Wiltshire, Savernake Forest, eastern border of Grand Avenue, approximately 1km NW of Eight Walks, from area of grass and moss, 17.ix.1981; Cornwall, St Austell, under hedge bordering china clay works, from aerial parts of couch grass plus 1cm of underlying roots and chalky soil, 9.xii.1981.

OTHER BRITISH RECORDS. IRE, Galway, Monivea wood, 20 miles NE of Galway, from litter and fermentation layers under pine, 21.viii.1981 (K P Martyn). ENGLAND, Kent, Westerham Caves, mixed deciduous/coniferous woodland (oak, beech, Scots pine) round main entrance of cave, from top 4cm of litter and fermentation layers, 1.ii.1981. SCOTLAND, Strathclyde, Loch Lomond, Inchcailloch island, area of understorey ferns, from litter and fermentation layers under oak, 13.ix.1982; Fair Isle, Furse, from moss on rocks, 9.vi.1964 (M. E. Bacchus). WALES, Dyfed, Rheidol Forest, approximately 20m from edge of forest, from top 4cm of bracken litter, 26.ii.1981.

REMARKS. Strandtmann was apparently unaware of the existence of *C. setosus* since he does not include it in any of his discussions of the genus (Strandtmann 1971, Strandtmann & Tilbrook 1968, Strandtmann & Prasse 1976). Examination of the respective holotypes showed them to be conspecific, with *C. setosus* taking priority.

Evans' description lacks many of the details now required for species identification and the above account serves to provide these additional data.

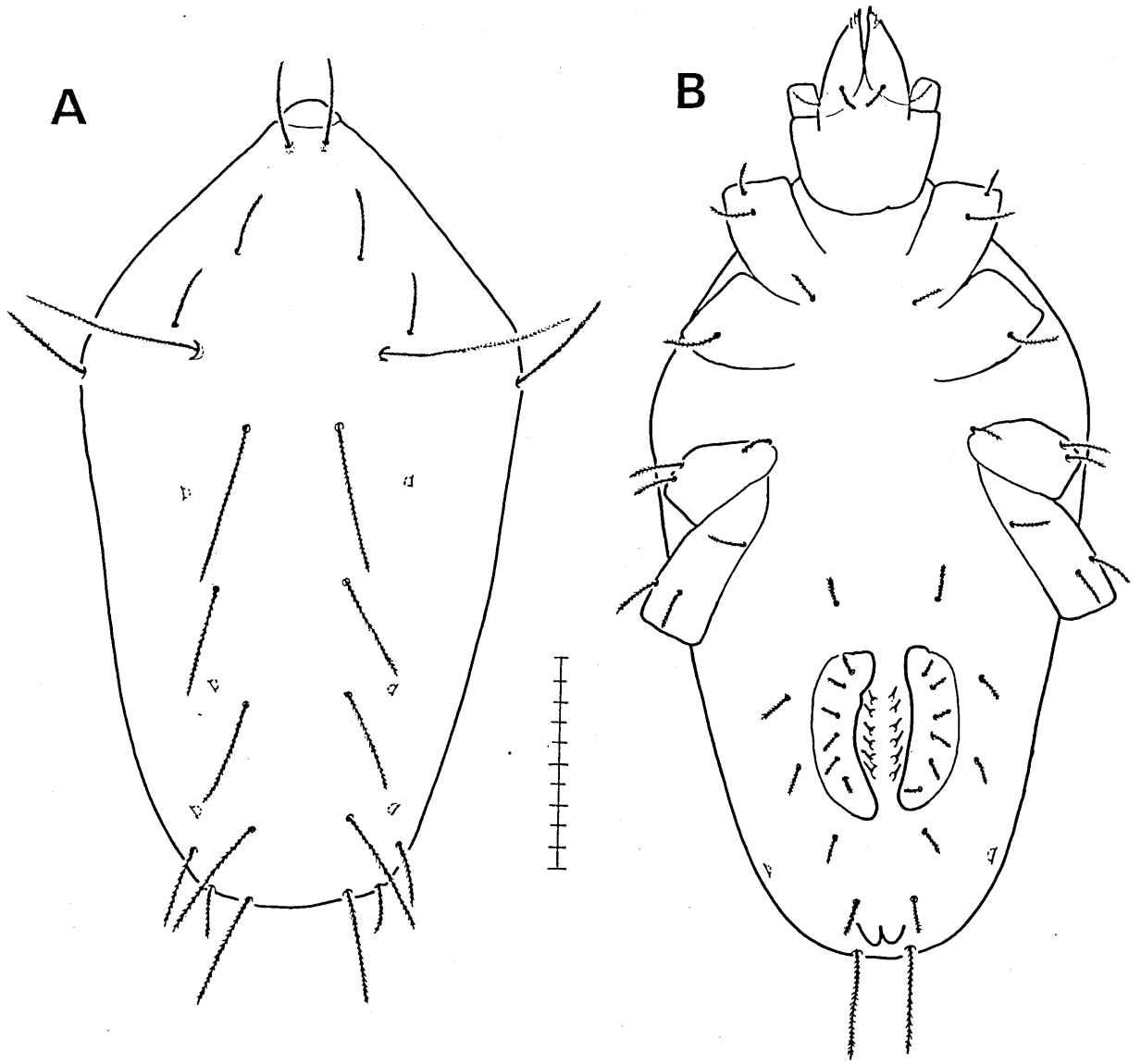
Fig. 84. *Cocceupodes setosus*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area ♂, sagittal.

Scale intervals 10µm.



C

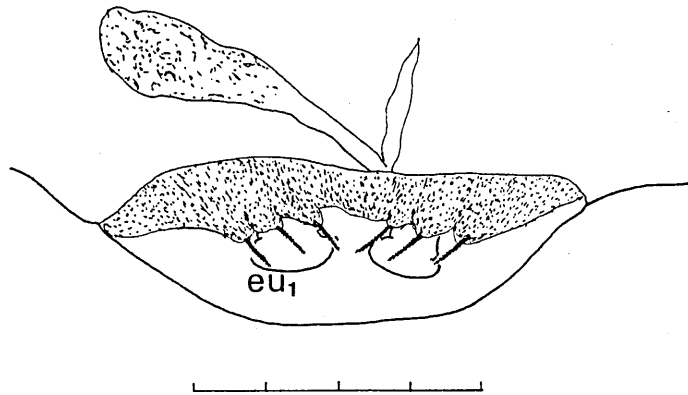
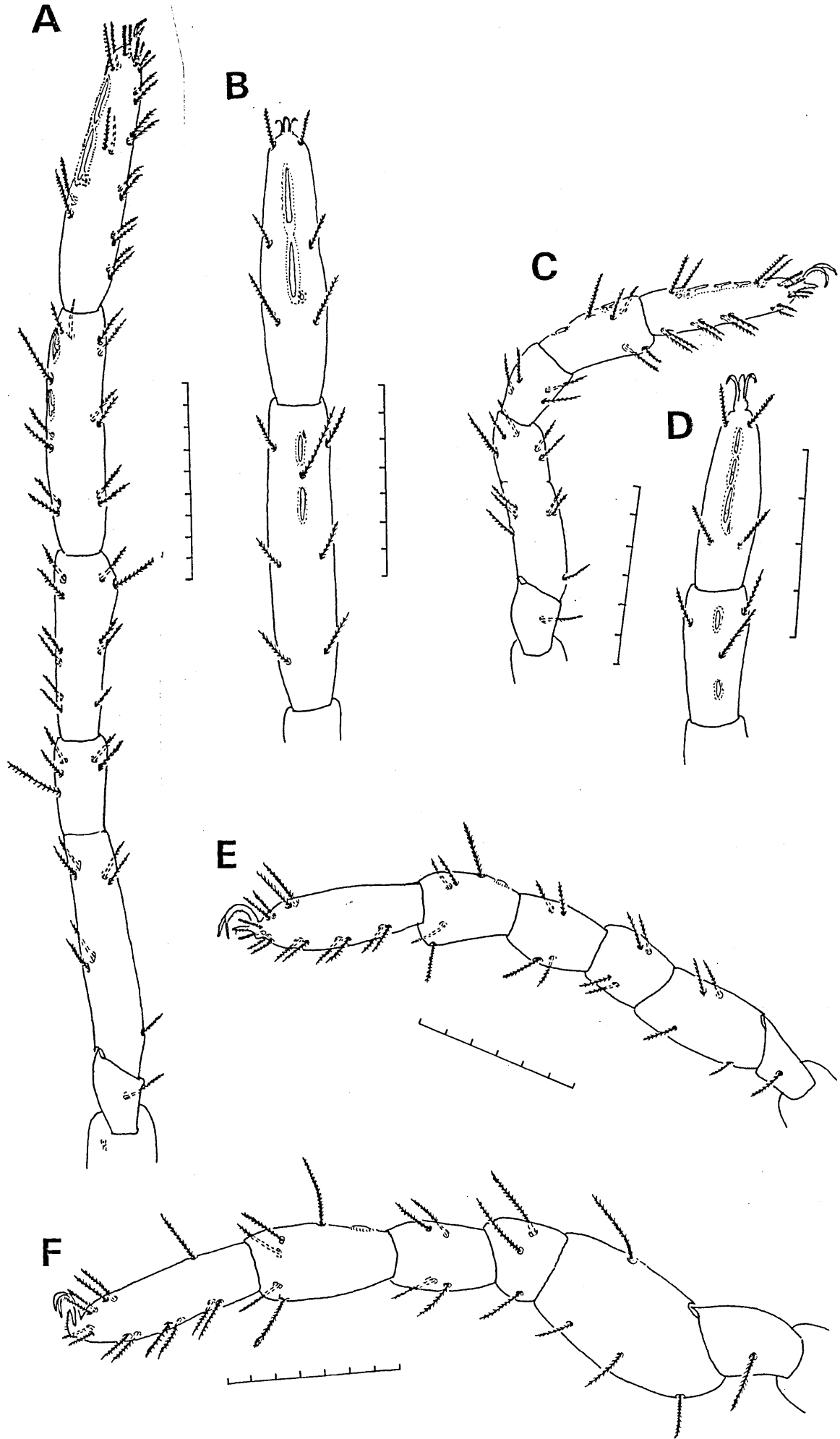


Fig. 85. *Cocceupodes setosus*:

- (A) leg I, posterolateral;
- (B) tarsus & tibia I, dorsal;
- (C) leg II, posterolateral;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Cocceupodes stellatus

Figs 86 & 87

Cocceupodes stellatus Strandmann & Prasse, 1976: 6.

DIAGNOSIS. This species can be distinguished from other members of the genus by the capitate internal vertical setae and the approximately obliquely arranged rhagidial organs on tarsus II.

New British record

Body length 314 (300-335), width 197 (191-203).

GNATHOSOMA. (Fig. 86B)

Subcapitulum: subcapitular setae ca. 11 long.

Palp: typical for genus.

Chelicera: total length 54 (49-57); *cha* ca. 6 long.

IDIOSOMA - DORSUM (Fig. 86A)

Naso: roughly triangular peak.

Setae: (*iv*) capitate, inserted just posterior to naso; lengths - (*iv*) 23 (20-25), (*ev*) 24 (22-27), (*T*) 73 (68-79), (*sc*) 34 (32-37), (*c*₁) 19 (17-22), (*c*₂) 56 (53-58), (*d*₁) & (*e*₁) subequal ca. 24 (21-27), (*f*₁) 37 (34-39), (*f*₂) 22 (19-25), (*h*₁) 46 (42-48), (*h*₂) 19 (17-23).

IDIOSOMA - VENTER (Fig. 86B)

Podosoma: (*1c*) 7 long, ca. third length *1a* & *b*; (*2a*) ca. 20; (*3a-c*) and (*4a-c*) both gradually increase in length distally from 9-15.

Genital area: six pairs eugenital, genital and aggenital setae, respectively ca. 7, 9 and 11 long.

Anal region: (*ps*₁) at 28 (25-29), approximately three times (*ps*₂).

LEGS (Fig. 87)

I approximately body length, II and III respectively just over and under half body length, IV approximately three-quarters body length.

Setae: formulae - I 1-12(7+5)-6-11-18, II 1-10(5+5)-4-5-13,

III 1-7(3+4)-4-5-12, IV 1-7(4+3)-4-5-11.

Solenidia & famuli: rhagidial organs of tarsus I slightly staggered parallel in separate pits, famulus located in separate pit posterolaterally and just posterior to proximal organ; rhagidial organs of tarsus II approximately obliquely parallel, famulus in separate pit posterolaterally about third of distance from base of proximal; organs of tibiae I and II in tandem and separate pits; one dorsoproximal rhagidial organ on tibiae III and IV.

MALE. Unknown.

DISTRIBUTION. England, German Democratic Republic, Scotland.

MATERIAL EXAMINED. Type material: Holotype ♀, GERMAN DEMOCRATIC REPUBLIC, Etzdorf/Saalkreis Experimental Farm, 1971 (J. Prasse) [MLU, slide no. 16]. British material: ENGLAND, Kent, Canterbury Nature Reserve, *Deschampsia/Agrostis* covering bank near power substation, from aerial parts of plants plus 2cm of underlying clay soil, 17.iii.1981; Cornwall, Goonhilly Downs, near Gweek, from moss off stone pillar under oak tree, 8.xii.1981.

OTHER BRITISH RECORDS. ENGLAND, Cambridgeshire, Woodwalton Fen, Compartment 36 (Fen Carr), from aerial parts of common comfrey and grass plus 2cm of underlying soil, 30.vi.1981; Surrey, Box Hill, Happy Valley, from mixed grasses plus underlying 1cm of soil, 2.vi.1982. SCOTLAND, Loch

Lomond Nature Reserve, in 20 acre field, from litter under hawthorn,
12.ix.1982; Grampian, Craigellachie, birch woodland with areas of boulders
covered with lichens, heather and moss, from moss mat covering rock,
17.ix.1982.

REMARKS. Strandtmann & Prasse (1976) remark on a similarity between *C. stellatus* and *C. communis* Shiba based on the form of the internal vertical setae and setal complement of the genital area. They quote a difference in the position of the famulus I and three and not two rhagidial organs on tarsus II. The latter point does not apply since Shiba corrected this to the normal generic complement of three (Shiba 1971).

Fig. 86. *Cocceupodes stellatus*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

Scale intervals 10 μ m.

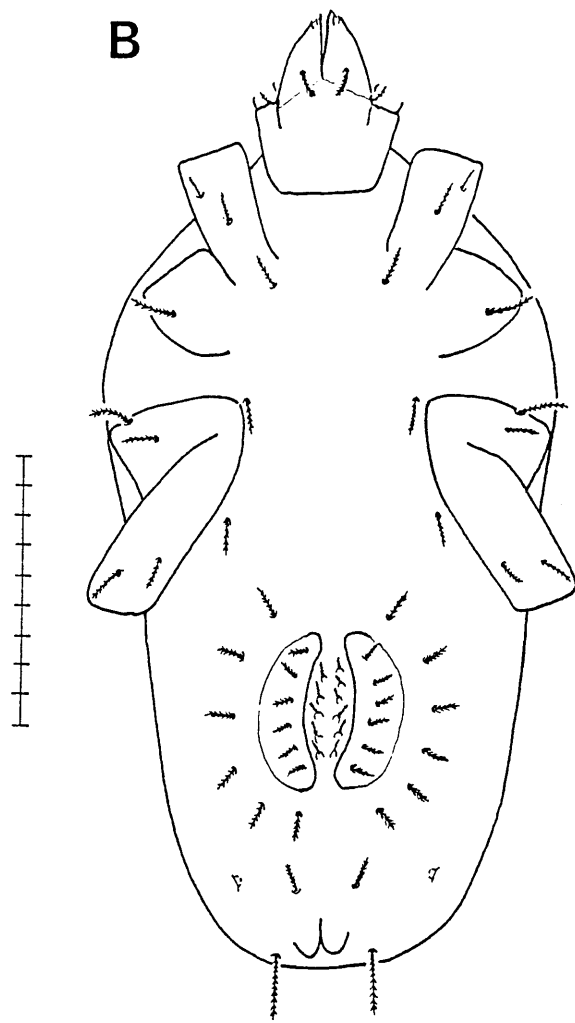
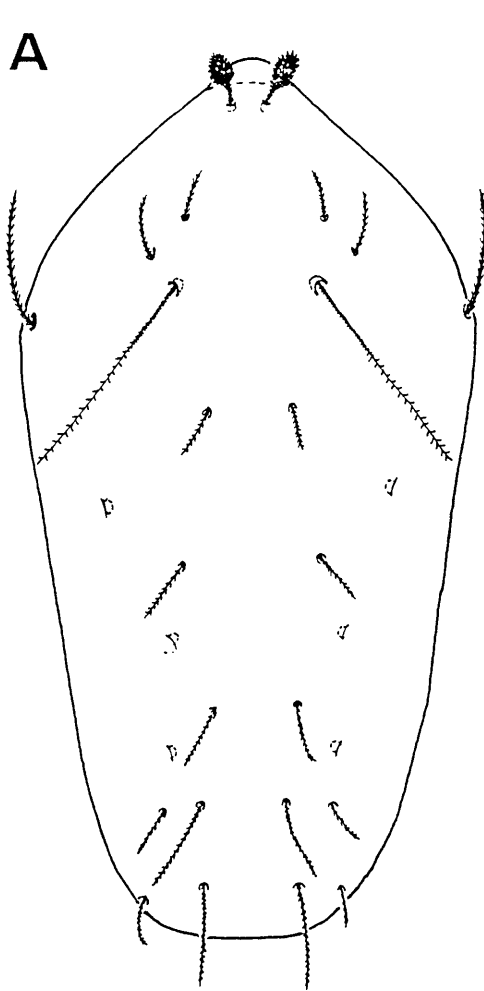
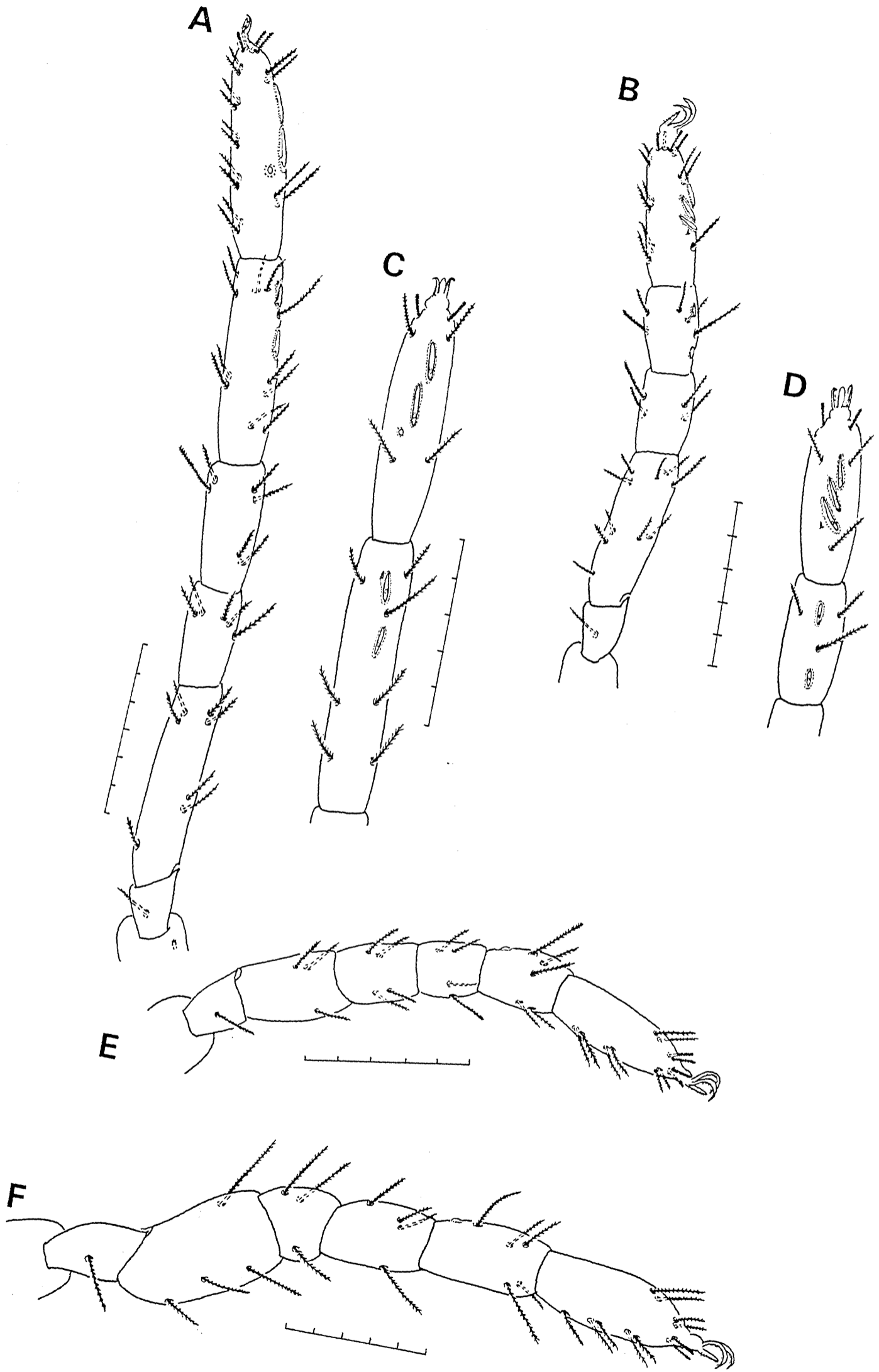


Fig. 87. *Cocceupodes stellatus*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Cocceupodes trisetatus Strandtmann & Prasse

Figs 16c, 21c, 25c, 88 & 89

Cocceupodes trisetatus Strandtmann & Prasse 1976: 7. Strandtmann & Goff, 1978: 34.

New British record

DIAGNOSIS. Differs from all other species of *Cocceupodes* by possessing only three pairs of genital setae in combination with simple internal vertical setae.

Body length 253 (220-280), width 117 (105-127).

GNATHOSOMA (Fig. 88B)

Subcapitulum: subcapitular setae ca. 10 long.

Palp: typical for genus.

Chelicera: total length 57 (53-61).

IDIOSOMA - DORSUM (Figs 16c, 21c, 88A)

Naso: small roughly triangular extension to the prodorsum.

Setae: (iv) simple, inserted markedly posterior to naso; mostly short, extending about halfway to base of posterior seta, although (c₂), (f₁) and (h₁) are noticeably longer; lengths - (iv) 38 (35-42), (ev) 13 (11-15), (T) 88 (84-91), (sc) 17 (15-20), (c₁) 14 (11-16), (c₂) 38 (35-41), (d₁) 17 (15-18), (e₁) 19 (16-21), (f₁) 33 (30-35), (f₂) 18 (15-20), (h₁) 32 (29-35), (h₂) 12 (9-14).

IDIOSOMA - VENTER (Figs 25c, 88B,D)

Podosoma: (1c) at 6 long, approximately third length of (1a & b), (2b)

ca. 21, (3a) at 12 approximately three-quarters length of subequal (3a & b), (4a) at 10 approximately two-thirds length subequal (4b & c).
Genital area: four pairs subequal eugenital setae, ca. 6 long; three pairs subequal genital setae, ca. 8; four pairs subequal aggenital setae, ca. 11.
Anal region: (ps₁) 27 (24-31), ca. three times longer than (ps₂).

LEGS (Fig. 89).

I 1.1 times body length, II and III respectively just above and below half body length, IV approximately three-quarters.

Setae: formulae I 1-13(8+5)-6-9-18, II 1-10(5+5)-4-5-14,
 III 1-7(3+4)-4-5-13, IV 1-6(3+3)-4-5-12.

Solenidia & famuli: rhagidial organs of tarsus I staggered parallel, famulus just posterolateral to base of proximal organ; tarsus II with organs in separate pits, parallel and in tandem, famulus posterolateral to proximal organ, in separate pit; tibia I with organs staggered parallel; tibia II with rhagidial organs proximal and distal.

MALE. (Fig. 88C) (5 specimens examined). Sperm sac clavate.

DISTRIBUTION. German Democratic Republic, England, Hawaii, Scotland, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, GERMAN DEMOCRATIC REPUBLIC, Etzdorf/Saalkreis Experimental Farm, 0-10cm soil under winter wheat, 1971 (J. Prasse) [MLU, slide no. 112]. **British material**: ENGLAND, Suffolk, ca. 1.5km SW of Walberswick, at edge of area of heathland, from mixture of predominantly *Agrostis* sp., *Cladonia* sp. & *Pleurozium schreberi*

plus underlying 1cm of soil, 7.i.1981; Westleton Heath, ca. 1km NE of Westleton, from aerial parts of *Calluna* sp. plus underlying 2cm of roots and soil, 9.i.1981.

OTHER BRITISH RECORDS. ENGLAND, Cornwall, Goonhilly Downs, near Gweek, from moss off stone pillar by road under oak tree, 8.xii.1981; Wiltshire, Savernake Forest, birch copse in eastern section of forest, with patchy understorey brambles, from moss round base of birch, 17.ix.1981; Yorkshire, Ilkley Moor, by Cow and Calf rocks, from *Polytrichum* moss between *Calluna* amongst rocks, 20.ii.1981. SCOTLAND, Strathclyde, Loch Lomond Nature Reserve, in 20 acre field, from debris and litter under hawthorn, 12.ix.1982; Fife, Abernethy Forest, from blueberry and moss amongst *Calluna* at edge of forest, 18.ix.1982. WALES, Dyfed, Cors Tregaron, West bog, raised *Sphagnum* bog, from *Eurynchium* sp. moss and *Agrostis* sp. under *Calluna*, 24.ii.1981.

REMARKS. Strandtmann & Prasse (1976) describe the rhagidial organs of tarsus I as being in tandem, while no mention is made of the famulus of tarsus II. Examination of the holotype revealed the arrangement of the rhagidial organs to be parallel and staggered, as in examples found in the British fauna, but the presence of the famulus could not be confirmed. However, since the famulus could only be observed in temporarily mounted specimens if the mite was orientated in just the right position, it is assumed that its presence was obscured in the holotype.

Fig. 88. *Cocceupodes trisetatus*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area ♂, sagittal;

(D) genital area ♀, sagittal.

Scale intervals 10µm.

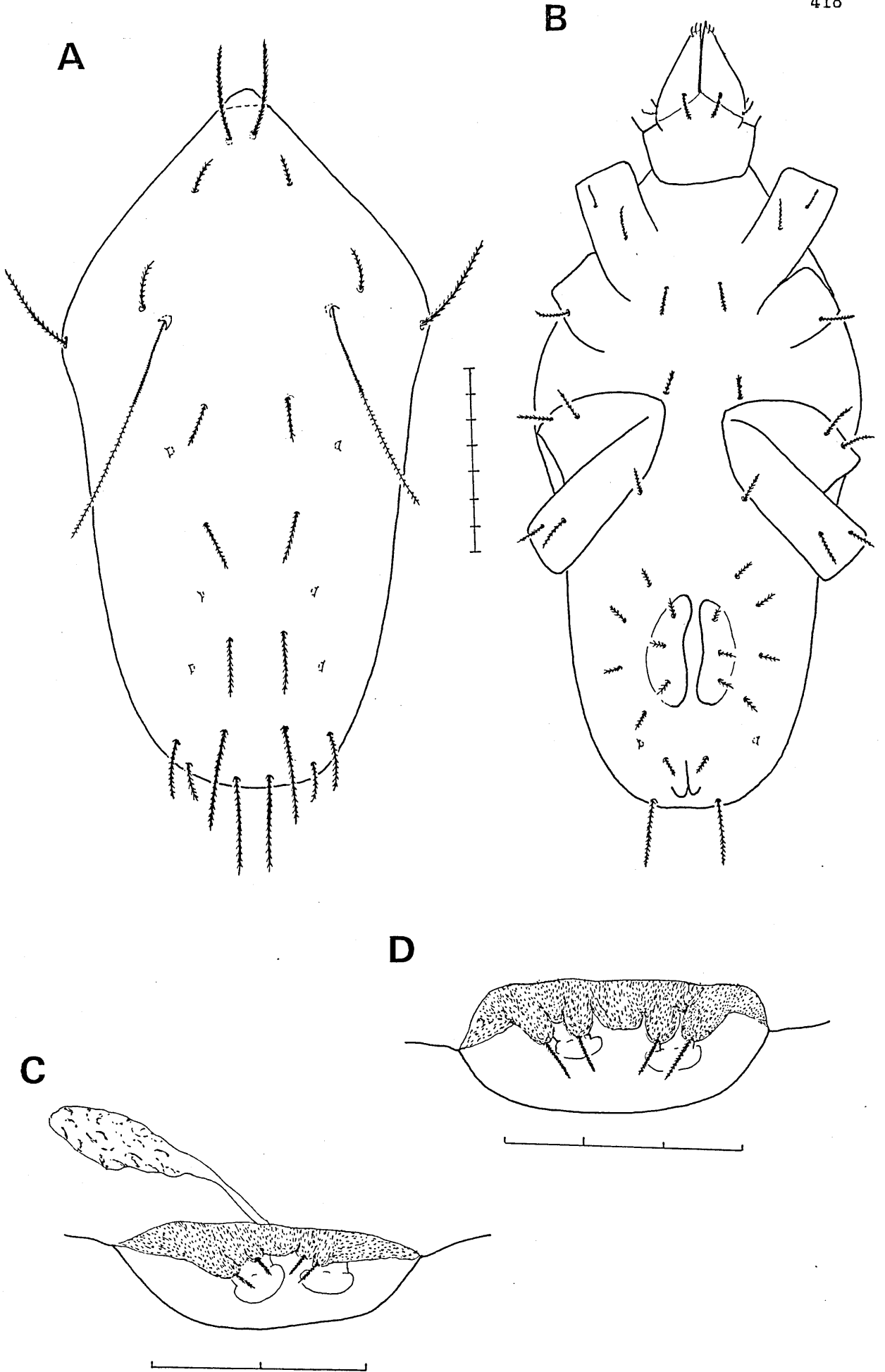
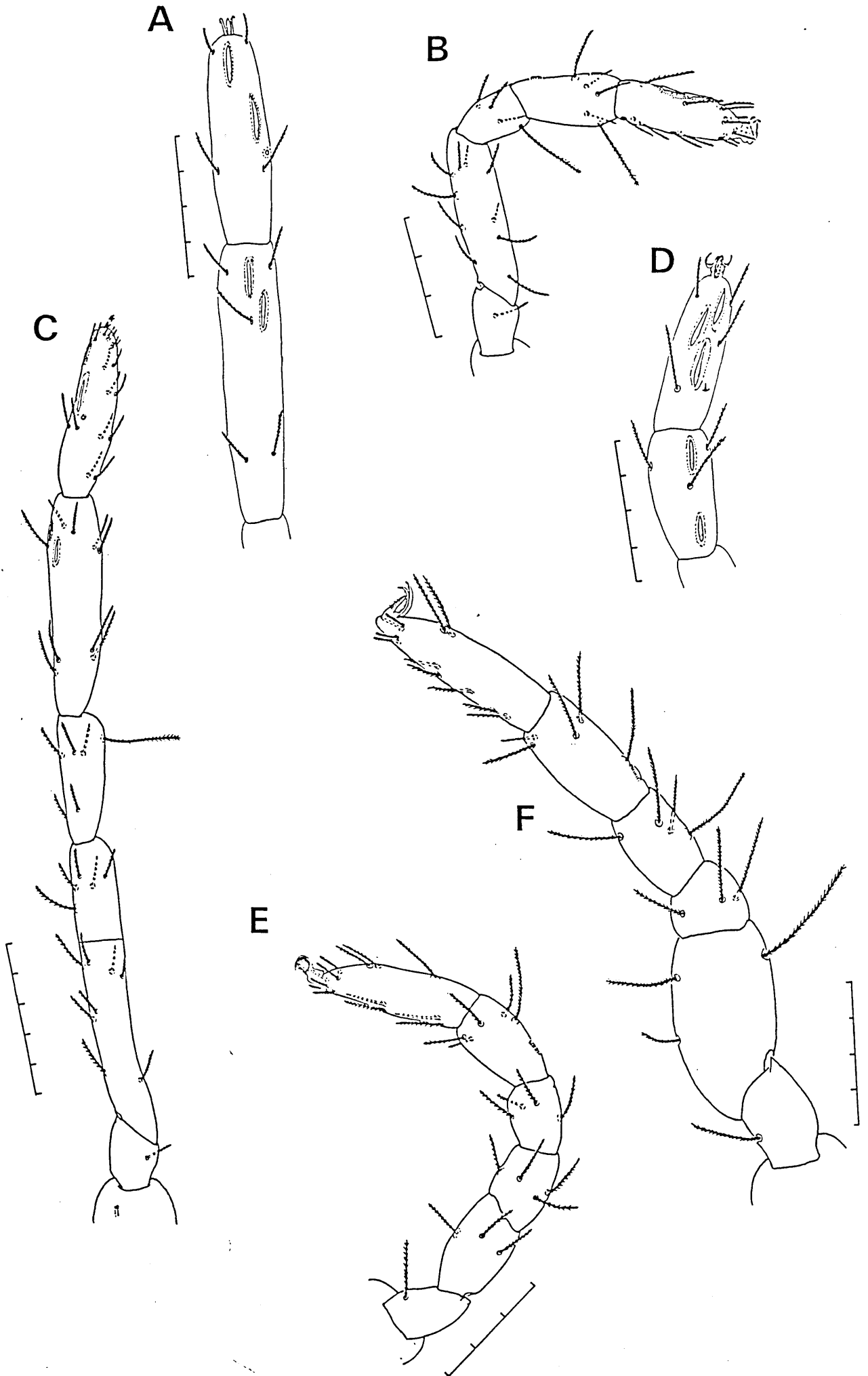


Fig. 89. *Cocceupodes trisetatus*:

- (A) tarsus & tibia I, dorsal;
- (B) leg II, posterolateral;
- (C) leg I, posterolateral;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.1.8 Genus *Linopodes* Koch

Linopodes Koch, 1835: 1; 1842: 66. Thor & Willmann, 1941: 37. Meyer & Ryke, 1960: 489. Strandtmann, 1971: 23.

DIAGNOSIS. This genus can immediately be distinguished from other eupodid genera by the extremely long and slender first pair of legs which are more than four times body length.

DEFINITION.

Small to medium (400-750).

Integument: weakly striate-spiculate, prodorsal shield with more densely spiculed striae, appendages spiculate.

Idiosomal form: lateral elements of opisthosomal segment C extend anteriorly round prodorsum; idiosoma not clearly subdivided, tapers slightly from shoulders to broadly rounded posterior.

GNATHOSOMA

Subcapitulum: long, slender, ratio length to width 1:0.3; (*sbc*₂) ca. two-thirds (*sbc*₁), former located ca. halfway between (*sbc*₁) and anterior limit of subcapitulum.

Palp: with slender tibiotarsus, length ca. three times greatest width; supracoxal seta with crown of spicules.

Chelicera: markedly slender; chela small, weakly chelate, both digits taper to point, account for eighth to tenth of total length; seta appears smooth under light microscope, comprised of filaments under SEM.

IDIOSOMA - DORSUM

Sejugal furrow represented by faint line of striae.

Nasq: a clear rounded rectangular lobe but not delimited dorsally by suture.

Setae: (iv) inserted on naso; (ev) three-quarters distance from (T) to anterior limit of prodorsum; (sc) markedly sublateral, just anterior and lateral to (T); (T) located at level of widest part of body; (c₂) occur approximately level with (T) and markedly anterior to (c₁); setae of f row approximately level; all short, not reaching base of posterior seta, simple, densely spinose; (T) filiform, spiculate particularly along distal two-thirds.

Lyrifissures: round.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-3-3; setae simple, densely spinose, blunt; (3a) and (4a) located on coxal margin.

Genital region with six pairs tapering, spiculated eugenital setae; six pairs spinose genital setae, (g₄) lateral to others; four pairs spinose aggenital setae.

Anal region: anus subterminal; two pairs pseudanal setae; lyrifissure (ih) located slightly laterally and approximately midway between (ag₄) and (ps₃).

LEGS.

Slender, I especially so and more than four times body length.

Setae: spinose, shorter than segments.

Solenidia & famuli: rhagidial organs T-shaped; tarsi I and II with respectively two and three rhagidial organs arranged in tandem but separate pits; tibiae I and II with two, those of I in tandem in distal third of segment, those of II proximal and distal; famulus of tibia I associated with distal organ.

Apotela: I markedly reduced, comprising two short hooks flanking slightly shorter pad-like empodium; remainder typical form, subequal.

MALES. Sperm sac clavate and unornamented or capitate and reticulate.

TYPE SPECIES. *Linopodes ravus* Koch

DISTRIBUTION. Cosmopolitan.

REMARKS. The date of establishment of both the genus and its type species, *L. ravus*, is usually quoted as 1836. Referral to Sherborn's list of publication dates for the 'Hefte' of Koch's *Deutschlands, Crustaceen, Myriapoden und Arachniden* shows that in both cases it should be 1835.

I consider *L. ravus* to be a *species inquirenda* but since Koch's figures of the species illustrates the characteristically long and slender first pair of legs, the current concept of *Linopodes* clearly conforms to Koch's idea.

Two species have been reported from the British Isles, *L. antennaepe*s (Austin 1937, Hussey 1963, Binns 1973) and *L. motatorius* (Hull 1918, Turk 1967, Hazelton 1970). The former is regarded to be a *species inquirenda* and so the identity of these specimens is uncertain.

Key to the British species of *Linopodes*

1. Leg I approximately four times body length; idiosomal setae extend ca. half intersetal distance; (f_2) and (h_2) noticeably finer than other setae *L. motatorius*
- Leg I approximately six times body length; idiosomal setae extend ca. two-thirds intersetal distance; (f_2) and (h_2) same form as other setae *L. agitatorius*

Linopodes agitatorius Canestrini

Figs 90 & 91

Linopodes agitatorius Berlese, 1916: 294.

DIAGNOSIS. *L. agitatorius* can be distinguished from the other member of the genus found in Britain by the first pair of legs being six times longer than the body and by the equally robust and relatively long idiodorsal setae which extend approximately two-thirds the intersetal distance.

Body length 680 (639-699), width 345 (339-357).

GNATHOSOMA (Figs 90C,D,E)

Subcapitulum: (*sbc*₁) at 47 long, approximately two-thirds longer than (*sbc*₂).

Palp: typical for genus.

Chelicera: total length 135 (124-141), chela accounting for approximately one tenth of this; *cha* 12 long.

IDIOSOMA - DORSUM (Fig. 90A)

Setae: lengths - (*iv*) 77 (69-84), (*ev*) 51 (46-54), (*T*) 128 (117-136), (*sc*) 42 (38-46), (*c*₁) 59 (56-61), (*c*₂) 71 (67-76), (*d*₁) 65 (61-68), (*e*₁) 67 (58-65), (*f*₁) 73 (69-78), (*f*₂) 57 (54-60), (*h*₁) 73 (68-77), (*h*₂) 56 (53-59).

IDIOSOMA - VENTER (Figs 90B,G)

Podosoma: (*1c*) at 42, approximately two-thirds (*1a & b*), (*2b*) 63, (*3a-c*) increase gradually in length from 42-50, (*4a-c*) increase in length gradually from 54-61.

Genital area: eugenital setae gradually increase in length from 18-30 long; genital setae subequal, ca. 24 long; aggenital setae decrease in length posteriorly from ca. 42-32.

Anal region: (ps_1) 61(57-65), (ps_2) just under half length.

LEGS (Fig. 91)

I six, II 1.5, III 1.4, IV 1.6 times body length.

Setae: formulae I 1-56(51+5)-18-22-24, II 1-25(20+5)-7-11-17, III 1-18(13+5)-7-11-17, IV 1-8(4+4)-8-11-16.

Solenidia & famuli: typical for genus.

MALE. (4 specimens examined) (Fig. 90F) Sperm sac capitate, reticulated.

DISTRIBUTION. East Africa, England, Scotland, Wales.

MATERIAL EXAMINED. Type material: EAST AFRICA, (Alluaud & Jeannel) [ISZA, slide no. 166/121. British material: ENGLAND, London, South Kensington, west garden of British Museum (Natural History), surface sample of grass, 1.iii.1982; Devon, Braunton Burrows, slacks between mature dunes, from moss by clump of *Carex* plus 2cm of underlying soil, 7.xii.1981. SCOTLAND, Highland, Rannoch Forest, from top 4cm of spruce litter, 15.ix.1982.

OTHER BRITISH RECORDS. ENGLAND, Wiltshire, Savernake Forest, birch copse in eastern part of forest with patchy understorey brambles, from moss round base of birch plus adhering soil, 17.ix.1981. WALES, Dyfed, Cors Tregaron, West bog, raised *Sphagnum* bog, from *Eurynchium* moss and *Agrostis* under *Calluna*, 24.ii.1981.

Fig. 90. *Linopodes agitatorius*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) chelicera, antiaxial, with *cha* enlarged
(drawn from scanning electron micrograph);
- (E) palp, antiaxial;
- (F) genital area σ^7 , sagittal;
- (G) genital area ρ , sagittal.

Scale intervals 10 μ m.

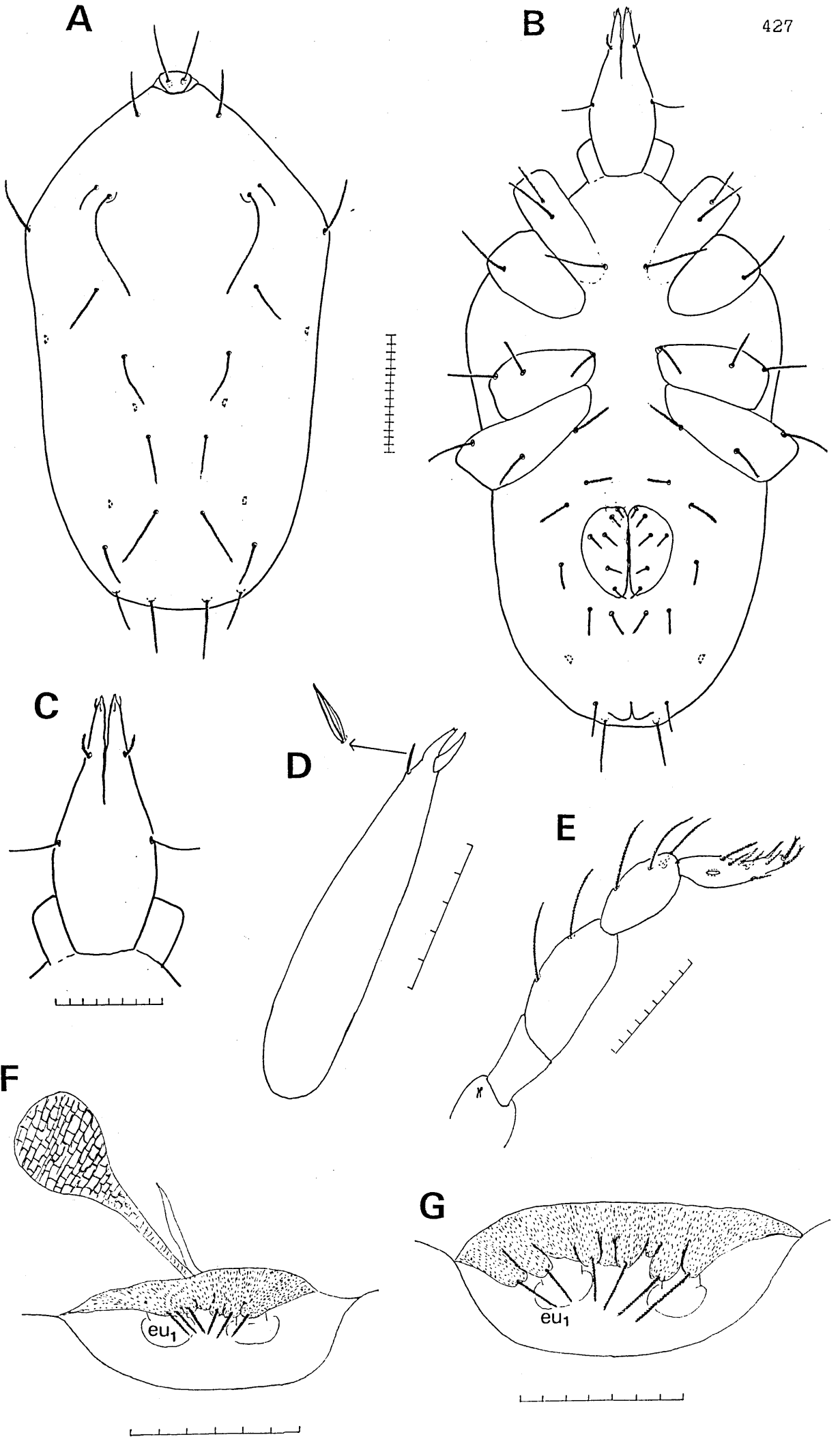


Fig. 91. *Linopodes agitatorius*:

(A) leg I, posterolateral;

(B) tarsus I, dorsal distal portion, showing position
of rhagidial organs;

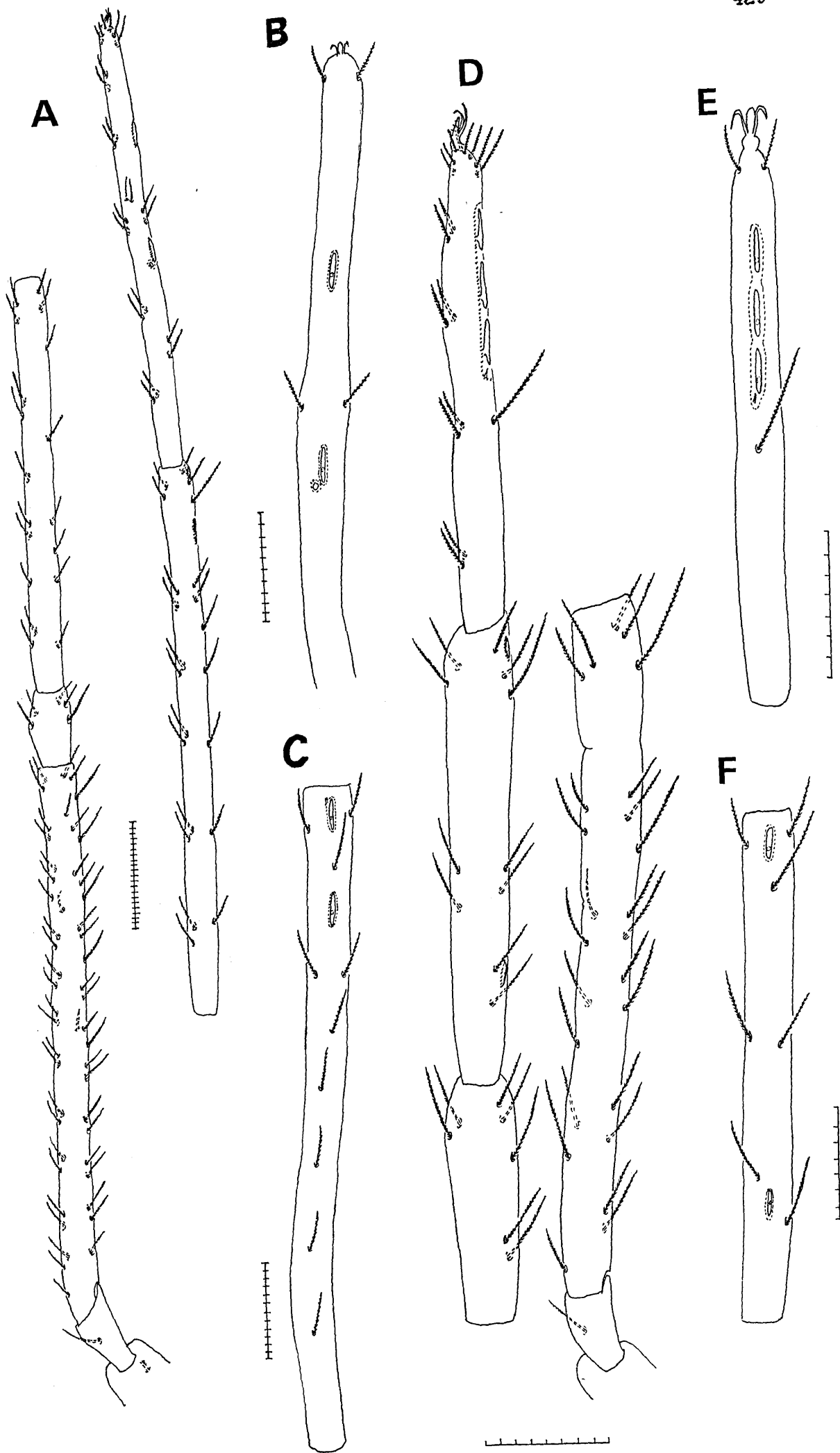
(C) tibia I, dorsal;

(D) leg II, posterolateral;

(E) tarsus II, dorsal;

(F) tibia II, dorsal.

Scale intervals 10 μ m.



Linopodes motatorius (Linnaeus)

Figs 92 & 93

Acarus motatorius Linnaeus, 1758: 616.*Linopodes motatorius*, Thor & Willmann 1941: 38.

DIAGNOSIS. Can be distinguished from the other British species of *Linopodes* by the first pair of legs being about four times longer than the body, the relatively short idiosomal setae and the more slender form of opisthosomal setae (f_2) and (h_2).

Body length 503 (438-569), width (156-350).

GNATHOSOMA (Fig. 92B)

Subcapitulum: (sbc_1), at ca. 25, approximately two-thirds length of (sbc_2).

Palp: typical for genus.

Chelicera: total length 116 (109-121)); chela account for ca. one eighth of length; cha 12 long.

DORSUM - IDIOSOMA (Fig. 92A)

Setae: (c_1) widely separated, h row almost terminal; (f_2) and (h_2) finer than other opisthosomal setae; lengths - (iv) 56 (46-63), (ev) 34 (28-37), (T) 97 (90-105), (sc) 25 (22-29), (c_1) 18 (16-21), (c_2) 43 (39-47), (d_1) 28 (25-32), (e_1) 30 (27-34), (f_1) 46 (43-50), (f_2) 40 (38-42), (h_1) 64 (59-67), (h_2) 45 (41-48).

IDIOSOMA - VENTER (Fig. 92B,C)

Podosoma: ($1c$) at 36, approximately two-thirds ($1a$ & b), ($2b$) 56, ($3a-c$) increase gradually in length from 37-44, ($4a-c$) increase gradually in length 50-59.

Genital area: eugenital setae (eu_5 & e_5) relatively slender, (eu_{1-3}) ca. 15 long, (eu_{4-5}) ca. 20; genital seta (g_3) longest at 25, remainder subequal,

ca. 19; aggenital setae gradually decrease in length posteriorly from ca. 37 to 29; four gravid specimens with two to four ovoid to circular eggs, 100 to 110 in diameter.

Anal region: (ps_1) 53 long, (ps_2) half as long.

LEGS (Fig. 93)

I four times, II 1.4 times, III 1.3 times, IV 1.6 times body length.

Setae: formulae I 1-43(39+5)-18-22-19, II 1-22(17+5)-5-9-15,

III 1-16(11+5)-6-9-15, IV 1-10(5+5)-6-9-15.

Solenidia & famuli: typical for genus.

MALE. (Fig. 92D) (5 specimens examined). Sperm sac clavate, unornamented.

DISTRIBUTION. Eire, England, Italy, Scotland, Wales.

MATERIAL EXAMINED. ITALY, Tuscany, Florence [ISZA, slide no. 144/271, from humus [ISZA, slide nos 152/35 & 371; Umbria, Bevagna [ISZA, slide no. 107/291. ENGLAND, Surrey, Box Hill, Happy Valley, from surface sample of grassland, 2.vi.1982. WALES, Dyfed, Rheidol Forest, from top 4cm of litter and fermentation layers under bracken, 26.ii.1982.

OTHER BRITISH RECORDS. EIRE, Galway, Ryehill, Monivea, 22 miles NE of Galway, beech copse, from hollow of beech tree, 20.viii.1981 (K. P. Martyn). SCOTLAND, Highland, southern shore of Loch Maree, near Kinlochewe, from birch and pine litter, 16.ix.1982; Strathclyde, western shore of Loch Lomond, by Edrich water, from moss, lichen and rotting wood under willow, 12.ix.1982.

REMARKS. This was a common species found in many wood- and grassland samples.

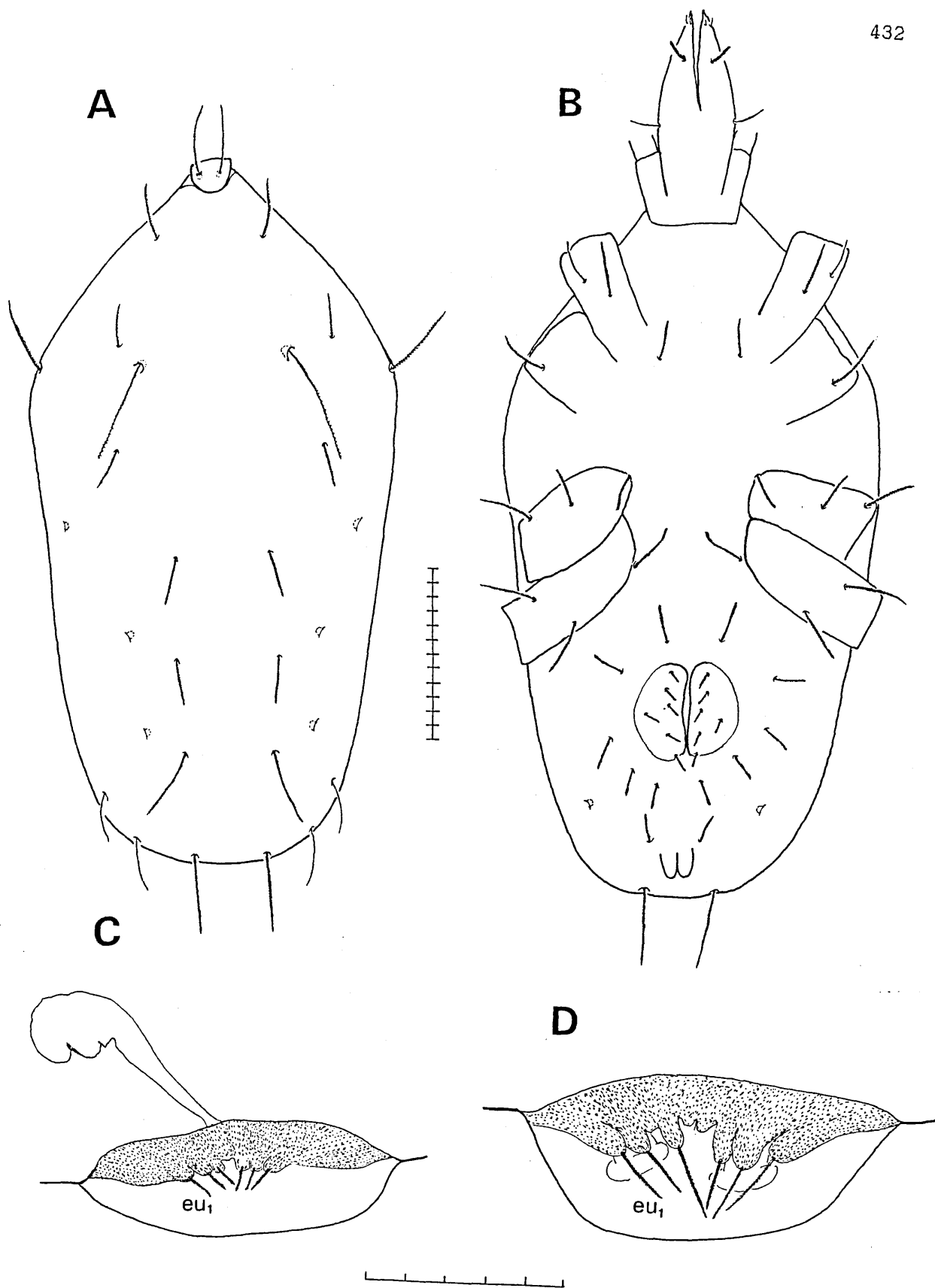


Fig. 92. *Linopodes motatorius*:

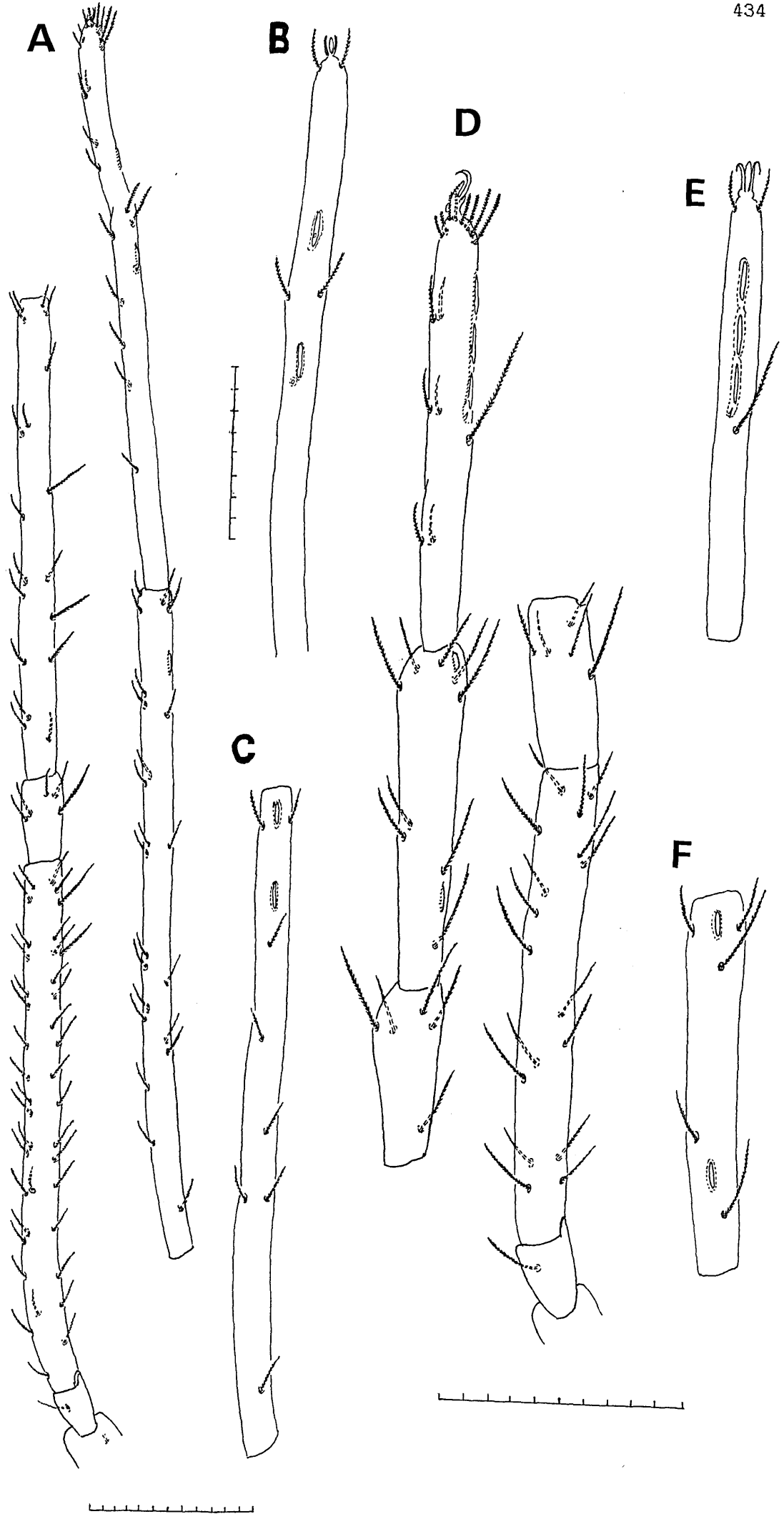
- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) genital area ♂, sagittal.
- (D) genital area ♀, sagittal.

Scale intervals 10 μ m.

Fig. 93. *Linopodes motatorius*:

- (A) leg I, posterolateral;
- (B) tarsus I, dorsal distal portion, showing position
of rhagidial organs;
- (C) tibia I, dorsal;
- (D) leg II, posterolateral;
- (E) tarsus II, dorsal;
- (F) tibia II, dorsal.

Scale intervals 10 μ m.



10.1.1.9 Genus *Subeupodes* n.gen.

Protereunetes Berlese, 1923: 245 [in part]. Thor & Willmann, 1941: 52 [in part]. Strandtmann, 1971: 82.

Eupodes: Strandtmann, 1970: 89 [in part].

DIAGNOSIS. *Subeupodes* can be distinguished from other genera of the Eupodidae by the combination of an ovoid palp tibiotarsus, three pairs of pseudanal setae and two rhagidial organs on tarsus II.

DEFINITION.

Small (279-330).

Integument: weakly striate-papillate, prodorsal shield and appendages papillate.

GNATHOSOMA.

Subcapitulum: ratio length to width 1:0.5; subcapitular setae subequal; (*sbc*₂) inserted approximately a quarter of distance from (*sbc*₁) to anterior limit of subcapitulum.

Palp with ovoid tibiotarsus, length *ca.* twice widest part; supracoxal seta weakly spiculated.

Chelicera: chela account for approximately one fifth of total length; *cha* smooth.

IDIOSOMA - DORSUM

Sejugal furrow: clearly subdivides idiosoma into roughly triangular prodorsum and opisthosoma which slightly tapers to broadly rounded posterior.

Naso: rounded rectangular, without delimiting dorsal suture.

Setae: (*iv*) inserted on naso; (*ev*) located approximately one fifth distance between (*T*) and anterior limit of prodorsum; (*sc*) just lateral and posterior to (*T*); setae of both *c* and *f* row level; (*T*) filiform, spiculated, markedly so in distal two-thirds; remaining setae short, spinose.

Lyrifissures: round.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-3; setae simple, spinose.

Genital area: four pairs tapering, densely spiculated eugenital setae; six pairs spinose genital setae, arranged in single file; four pairs spinose aggenital setae.

Anal region: anus subterminal; three pairs pseudanal setae; (*ih*) located laterally and just anteriorly to (*ps₃*).

LEGS

Slender, all shorter than body.

Setae: spinose, shorter than segments; complements vary only by one or two setae in tarsus I, genu and tibia III, trochanter, genu and tarsus IV.

Solenidia & famuli: rhagidial organs T-shaped; two rhagidial organs on both tarsus I and II, variously arranged; famuli located in same pit just posterolateral to proximal organ; tibia I and II both with one proximal and one distal rhagidial organ; genual solenidia present.

Apotele: all of similar form.

MALE. Sperm sac clavate, unornamented but bulb sometimes with granular appearance.

TYPE SPECIES. *Protereunetes boernerii* Thor

ETYMOLOGY. The generic name is derived from the latin 'sub', meaning somewhat less than, and pertains to the similarity to but smaller form of the members compared to those of the genus *Eupodes*.

DISTRIBUTION. Alaska, Antarctica, England, Norway, Wales.

REMARKS. The species classified in this genus would traditionally have been included in the now invalid genus *Protereunetes* Berlese but the differences in the form of the palp tibia-tarsus and in the solenidiotaxy were considered sufficient to erect a separate genus to accommodate them. The species *Subeupodes parvus* (Booth *et al* 1985) **n.comb.** is also classified in this genus.

Subeupodes boernerii (Thor) n.comb.

Figs 94 & 95

Protereunetes boernerii Thor, 1934b: 129.*Protereunetes boernerii*: Thor & Willmann, 1941: 54; Strandtmann, 1971: 83.

DIAGNOSIS. Can immediately be distinguished by the oblique rhagidial organs on tarsus II.

Body length 295 (279-308), width 163 (159-171).

GNATHOSOMA (Fig. 94B,C,D)Subcapitulum: subcapitular setae ca. 8 long.Palp: typical for genus.Chelicera: total length 44 (41-46); *cha* smooth, ca. 8.**IDIOSOMA - DORSUM** (Fig. 94A)

Idiosomal setae: lengths - (*iv*) 5 (4-7), (*ev*) and (*sc*) subequal ca. 11, (*7*) 29 (26-31), (*c₂*) 15 (13-16), remaining setae increase in length gradually posteriorly from ca. 8 to 17.

IDIOSOMA - VENTER (Fig. 94B,E)

Podosoma: (*2b* at ca. 16, (*1c*) at 7 long approximately two-thirds length of remainder.

Genital area: eugenital setae short, ca. 4; genital setae subequal ca. 7 long; aggenital setae subequal, ca. 9 long.

Anal region: (*ps₁*) 15, slightly longer than (*ps₂*) and approximately twice as long as (*ps₃*).

LEGS (Fig. 95)

I two-thirds body length, II and III just under half, IV three-quarters body length.

Setae: spinose to plumose; formulae - I 1-12(7+5)-6-5-21,
II 1-10(5+5)-4-5-13, III 1-8(4+4)-4-5-12, IV 1-6(3+3)-4-5-13.

Solenidia & famuli: tarsal I rhagidial organs in confluent pits, proximal approximately three times length of distal; those of tarsus II obliquely parallel in separate pits, proximal subtended by famulus, distal organ approximately half length of proximal; tibia I and II with obliquely positioned rhagidial organs; genua I to III with dorsomedian erect solenidion; tibia IV with dorsoproximal rhagidial organ.

MALE. (Fig. 94F) (4 specimens examined). Sperm sac clavate, unornamented, in some specimens has granular appearance.

DISTRIBUTION. Alaska, England, Norway, Wales.

MATERIAL EXAMINED. ENGLAND, Suffolk, Westleton Heath, from aerial parts of *Calluna* plus underlying 2cm of roots and soil, 9.i.1981; Berkshire, Windsor Forest, from litter inside hollow in oak tree, 4.i.1976 (P. D. Hillyard).

OTHER BRITISH RECORDS. ENGLAND, Cornwall, approximately 500m from eastern exit of Bicton Woods, south-facing hedgerow bordering pasture, including hawthorn, *Rubus* and ivy, from litter under hedge, 8.xii.1981.
WALES, Dyfed, Cors Tregaron, from clump of *Cladonia* under *Calluna* on edge of hummock in West bog, 24.i.1981.

REMARKS. Type material of *S. boernerii* does not exist while its description lacks many of the details now found necessary for determinations (Thor 1934b). The specimens examined here, however, fit

Thor's figure and description and, furthermore, are conspecific with other material (Strandtmann 1971) identified as *Protereunetes boernerii* and I consequently see no reason to introduce a new specific name.

S. boernerii was an uncommon species, found only from the above localities.

Fig. 94. *Subeupodes boernerii*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) palp, antiaxial;
- (D) chelicera, antiaxial;
- (E) genital area σ^7 , sagittal;
- (F) genital area ϱ , sagittal.

Scale intervals 10 μ m.

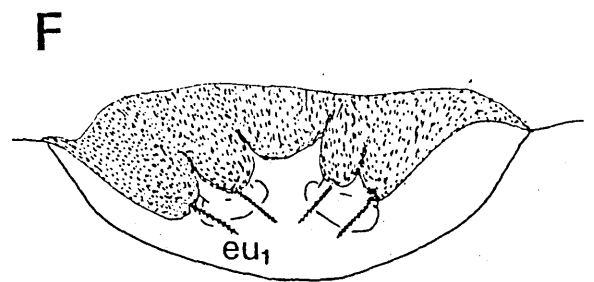
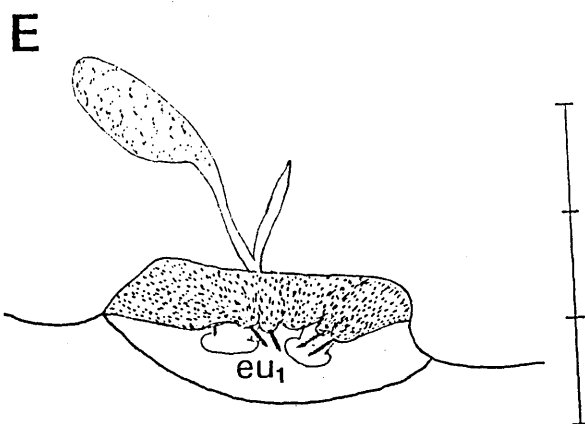
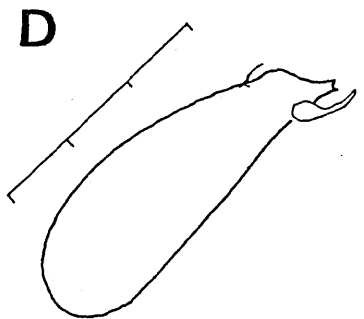
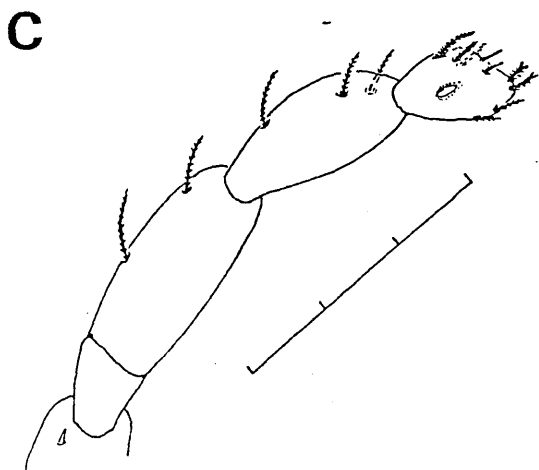
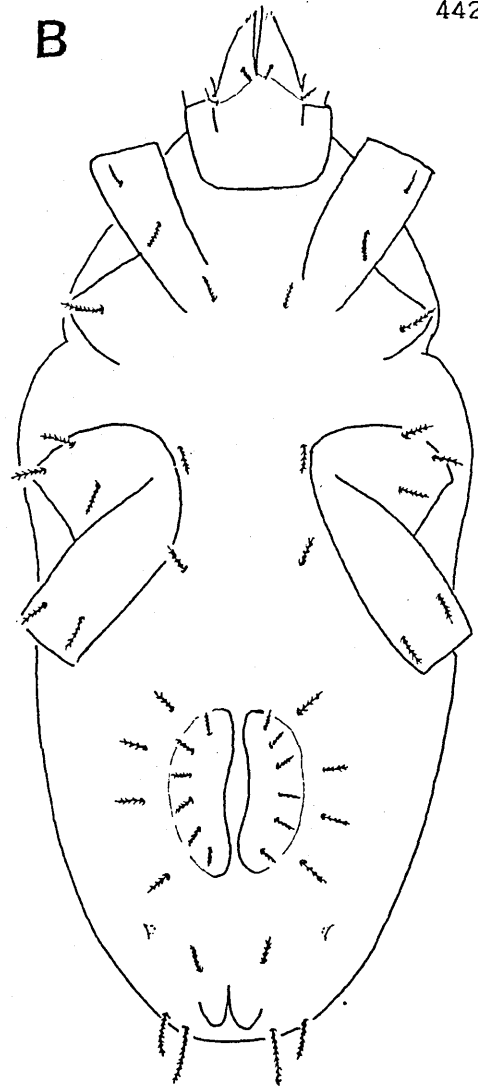
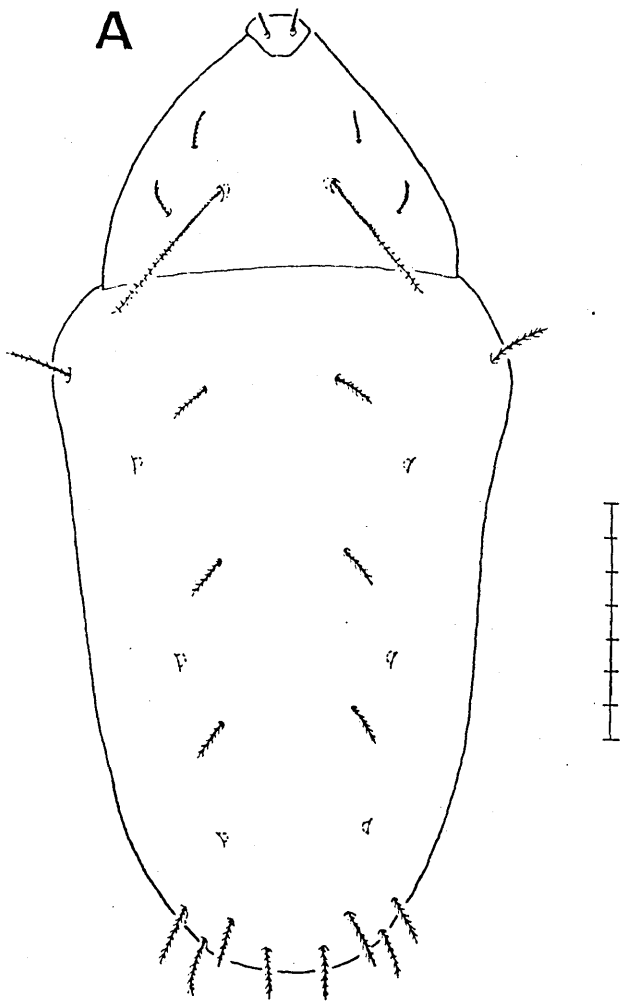
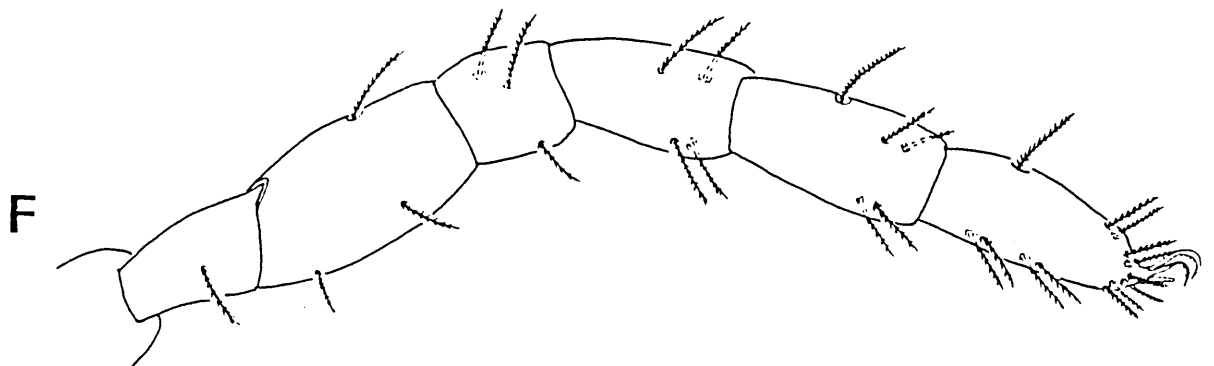
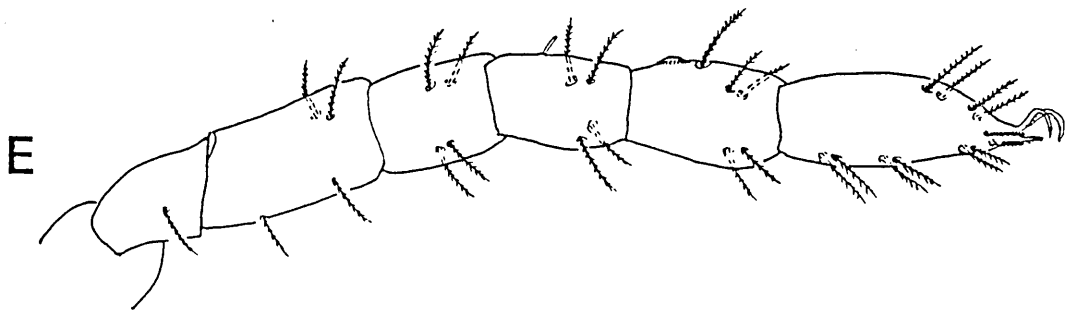
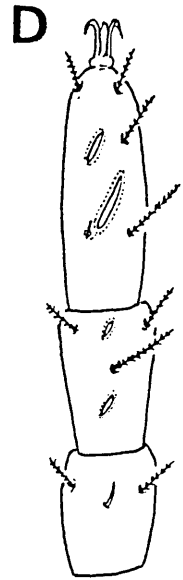
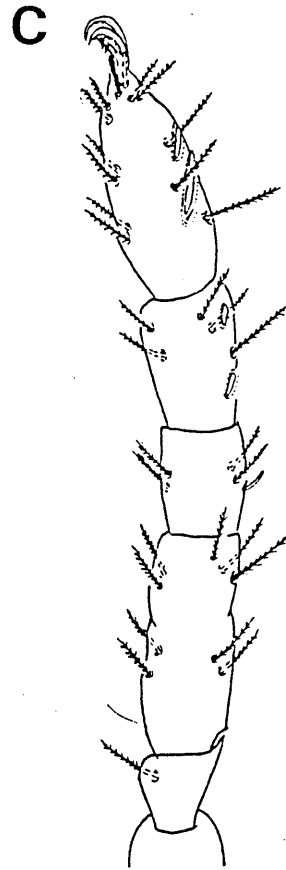
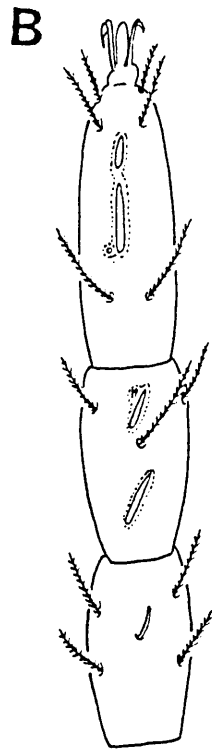
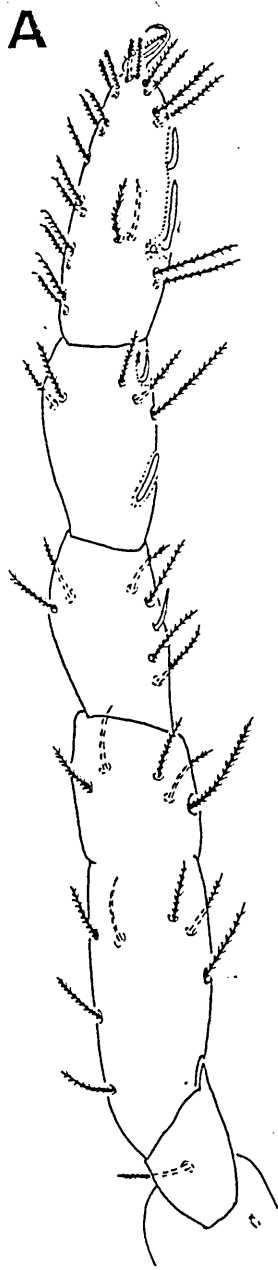


Fig. 95. *Subeupodes boernerii*:

- (A) leg I, posterolateral;
- (B) tarsus & tibia I, dorsal;
- (C) leg II, posterolateral;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.2 Family Penthaleidae Oudemans

Penthaleidae Oudemans, 1931: 252 [in part]. Thor & Willmann, 1941: 73.

Wainstein, 1978: 110. Strandtmann, 1981: 392. Kethley 1982: 121.

Eupodidae: Baker & Wharton, 1952: 174 [in part].

DIAGNOSIS. The family can immediately be distinguished from the other eupodoid families by the weakly to strongly neutrichous chaetome and the short, robust palps.

DEFINITION.

Small to large (350-1000), lightly sclerotized.

Integument of idiosoma weakly striate-spiculate, striae of prodorsal shield more densely spiculated; appendages spiculate.

Chaetome: weakly to strongly neutrichous.

GNATHOSOMA.

Subcapitulum: subcapitular setae approximately level midway on subcapitulum; two pairs minute, smooth adoral setae.

Palp: short and robust, length of tibia-tarsus approximately equal to breadth; tibia-tarsus with rhagidial organ anti-axially; *1'* spiralled, remainder spinose; supracoxal seta papillate.

Chelicera: chela account for approximately one-fifth of total length; movable digit scimitar-like, fixed digit terminates in three finger-like processes or fixed digit with shallow fork and movable digit slightly hooked; *cha* located dorsally just proximal to chela.

IDIOSOMA - DORSUM

Sejugal furrow indistinct, not subdividing globular idiosoma.

Naso: clearly delimited from prodorsum by suture.

Setae: (iv) located on naso; (D) filiform, spiculated, other setae smooth (although weakly serrate under SEM) to spinose.

Lyrifissures round.

IDIOSOMA - VENTER

Podosoma: clearly but faintly defined, proximal margins of I and II sometimes indistinct, never meet medially; II and III on either side of the body sometimes contiguous; numbers of setae variable.

Genital area: eugenital setae never heteromorphic; shields roughly semi-circular, outer margins indistinct; most genital setae arranged in line near free edge of shield, but with a variable number randomly distributed just lateral to these; ovipositor present; sperm sac clavate and unornamented or capitate and reticulated.

Anal region: anus dorsal and circular, drawn up into short collar or terminal and slit-like; three pairs pseudanal setae; *ih* dorsolateral or ventral.

LEGS.

Up to twice body length; slender.

Solenidia & famuli: rhagidial organs L-shaped, some semi-erect, three on tarsi I and II, one on tibiae I and II; famuli never elaborate; spiniform solenidia long and blunt, sometimes numerous and occur on most leg segments.

Apotela: of similar form.

TYPE GENUS. *Penthaleus* Koch

DISTRIBUTION. Cosmopolitan.

Genera classified in the family Penthaleidae

Penthaleus Koch 1835

Halotydeus Berlese 1891

Linopenthaloides Strandtmann 1981

Key to the genera of the family Penthaleidae

1. Coxae II and III contiguous; anus slit-like, terminal

* *Linopenthaloides*
- Coxae II and III separated; anus circular and dorsal or slit-like and terminal 2
2. Anus circular and dorsal; body setae smooth; strongly neutrichous

Penthaleus
- Anus slit-like and terminal; body setae spinose; weakly to moderately neutrichous † *Halotydeus*

* Genus not recorded from the British fauna.

† Genus recorded in Turk (1953) but not found in this study.

10.1.2.1 Genus *Penthaleus* Koch

Penthaleus Koch, 1835: 12; 1842: 63. Thor & Willmann, 1941: 76. Kethley, 1982: 121.

DIAGNOSIS. This genus can be distinguished from other penthaleid genera by the strongly neutrichous chaetome, the smooth setae and the dorsal, circular anus.

DEFINITION.

Small to large (370-1000); lightly sclerotized.

Integument: idiosoma weakly striate-spiculate; prodorsal shield present, with striae more heavily spiculated; appendages spiculated.

Chaetome: strongly neutrichous.

Idiosomal form: rounded, not clearly subdivided into prodorsum and opisthosoma.

GNATHOSOMA.

Subcapitulum: ratio length to width 1:0.6; subcapitular setae smooth subequal, located at same level approximately midway on subcapitulum.

Palp: up to four setae on palp femur and genu.

Chelicera: chela account for approximately one fifth of total length; fixed digit terminates in three finger-like processes; movable digit sickle-shaped; *cha* smooth.

IDIOSOMA - DORSUM

Eyes: sometimes present as semi-circular or circular outline but not discernible under SEM.

Sejugal furrow present as narrow band of transverse striae.

Setae: (7) relatively short, weakly spiculated or smooth; setae smooth under light microscope, weakly serrated under SEM; neotrichy and dorsal position of anus prevents identification of homologues of other eupodoids.

Lyrifissures: round.

IDIOSOMA - VENTER

Podosoma: setae simple, smooth; up to eight on each coxa.

Genital area: six pairs smooth homeomorphic eugenital setae; genital setae more or less in two rows or randomly distributed; genital and aggenital setae smooth, simple.

Anal region: anus dorsal, circular, drawn up into collar; associated setae smooth, simple, (*ih*) dorso-laterally, ca. midway between anus and posterior margin of body.

LEGS.

I shorter than or up to twice body length; all segments slender.

Setae: all short; prorals, unguinals, ventral and lateral setae spinose, remainder smooth.

Solenidia & famuli: three tarsal rhagidial organs present, usually semi-erect; famuli variously located; several long blunt erect solenidia present on all tibiae and genua and often also on tarsi, in addition to rhagidial organs on I and II.

TYPE SPECIES. *Penthaleus haematopus* Koch *sp.inq.*

DISTRIBUTION. Cosmopolitan.

REMARKS. Koch established the genus *Penthaleus* by indication in 1835 and not 1836 as is the usually quoted date. As was the case for the genera

Eupodes and *Linopodes*, the type species of *Penthaleus* was not adequately described to permit identification. However, Koch's figure of *P. haematopus*, clearly indicates that the current concept of the genus conforms to that of Koch.

Three species of *Penthaleus* have previously been recorded from the British Isles (Hull 1918, Halbert 1915). Of these, I consider both *P. haematopus* Koch and *P. ovatus* Koch to be *species inquirendae* due to their cursory descriptions, while the third species, *P. longipilis* (Canestrini), was collected during the present study.

The neotrichous chaetome and dorsal anus of postlarval stages of *Penthaleus* prevent the identification of the homologues of idiosomal setae of holotrichous eupodoids. However, examination of the larval stage, in which neotrichy has not yet developed and the anus is terminal, reveals the normal arrangement of setae and lyrifissures and allows the complement of three pairs of pseudanal setae to be discerned (see section 11).

In the following account of the British species, diagnoses only refer to British species since it has not been possible to confirm the validity of many of the nominate species of *Penthaleus*.

Key to the British species of *Penthaleus*

1. Large, idiosoma more than 800 long; idiosomal setae longer than intersetal distance *P. longipilis*
- Small, idiosoma less than 500 long; idiosomal setae shorter than intersetal distance *P. minor*

Penthaleus longipilis (Canestrini)

Figs 96 & 97

Notophallus longipilis Canestrini, 1886: 706.

DIAGNOSIS. *P. longipilis* can be distinguished from the other British species of the genus by its larger size and much longer setae.

Body length 890 (878-921), width 691 (678-704).

GNATHOSOMA (Figs 96C,D,E)

Subcapitulum: subcapitular setae subequal ca. 58 long.

Palp: setal formula 4-4-9.

Chelicera: total length 157 (150-163); *cha* ca. 11 long.

IDIOSOMA - DORSUM (Fig. 96A)

Setae: strongly neotrichous, with respectively 18-21 and 49-55 setae on the prodorsum and opisthosoma; (*T*) 102 (94-107), remainder 88-95 long, clearly overlap each other.

IDIOSOMA - VENTER (Figs 96B,F)

Podosoma: setal number varies on either side of body and between specimens, ranges as follows - I 7-10, II 4-6, III 7-19, IV 5-7, approximately 25 setae scattered between coxae; setae smooth, subequal 55-60 long.

Genital area: six pairs smooth eugenital setae, subequal ca. 38 long; 12-16 pairs smooth genital setae, ca. 49 long, arranged loosely in two longitudinal rows; 30-38 setae surrounding genital shields, not all forming pairs, smooth ca. 55 long.

Anal region: anus surrounded by numerous smooth setae.

LEGS (Fig. 97)

I and IV approximately body length, II and III respectively just below and above two-thirds body length.

Setae: strongly neutrichous.

Solenidia: tarsi with three semi-erect rhagidial organs on distal third of segment plus three dorsal erect solenidia arranged in tandem along proximal half; tibiae to femora all with three or four dorsal erect solenidia.

MALE. Unknown.

DISTRIBUTION. Eire, England, Italy.

MATERIAL EXAMINED. ITALY: Belluno, from moss, [ISZA, slide nos 46/11, 49/35, 50/44], Montello, from moss [ISZA, slide nos 46/12-13], Umbria, Bevagna [ISZA, slide nos 108/1-5]. British material: ENGLAND, Leicestershire, 12km south of Hinkley, area of oak wood edged by hawthorn hedge, from hedgerow litter, 19.ii.1982; Suffolk, Hollesley Common, from moss and litter by pine stump, 24.ii.1984.

OTHER BRITISH RECORDS. EIRE, Clare, Lough Inchiquin, Bushy Island, from humus round shore debris, 26.vi-10.vii.1971 (P.N. Lawrence); ENGLAND, Kent, Dungeness, patch of broom ca. 350m south-east of power station, from mat of moss (*Polytrichum*) and lichen (*Cladonia*) under broom, 18.iii.1981.

REMARKS. Type material of this species was not made available for study but, since the British material was conspecific with named specimens examined in Berlese's collection, I have utilized the same name i.e. *P. longipilis*.

Fig. 96. *Penthaleus longipilis*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

Scale intervals 100 μ m.

(C) subcapitulum, venter;

(D) palp, antiaxial;

(E) chelicera, antiaxial;

(F) genital area φ , sagittal.

Scale intervals 10 μ m.

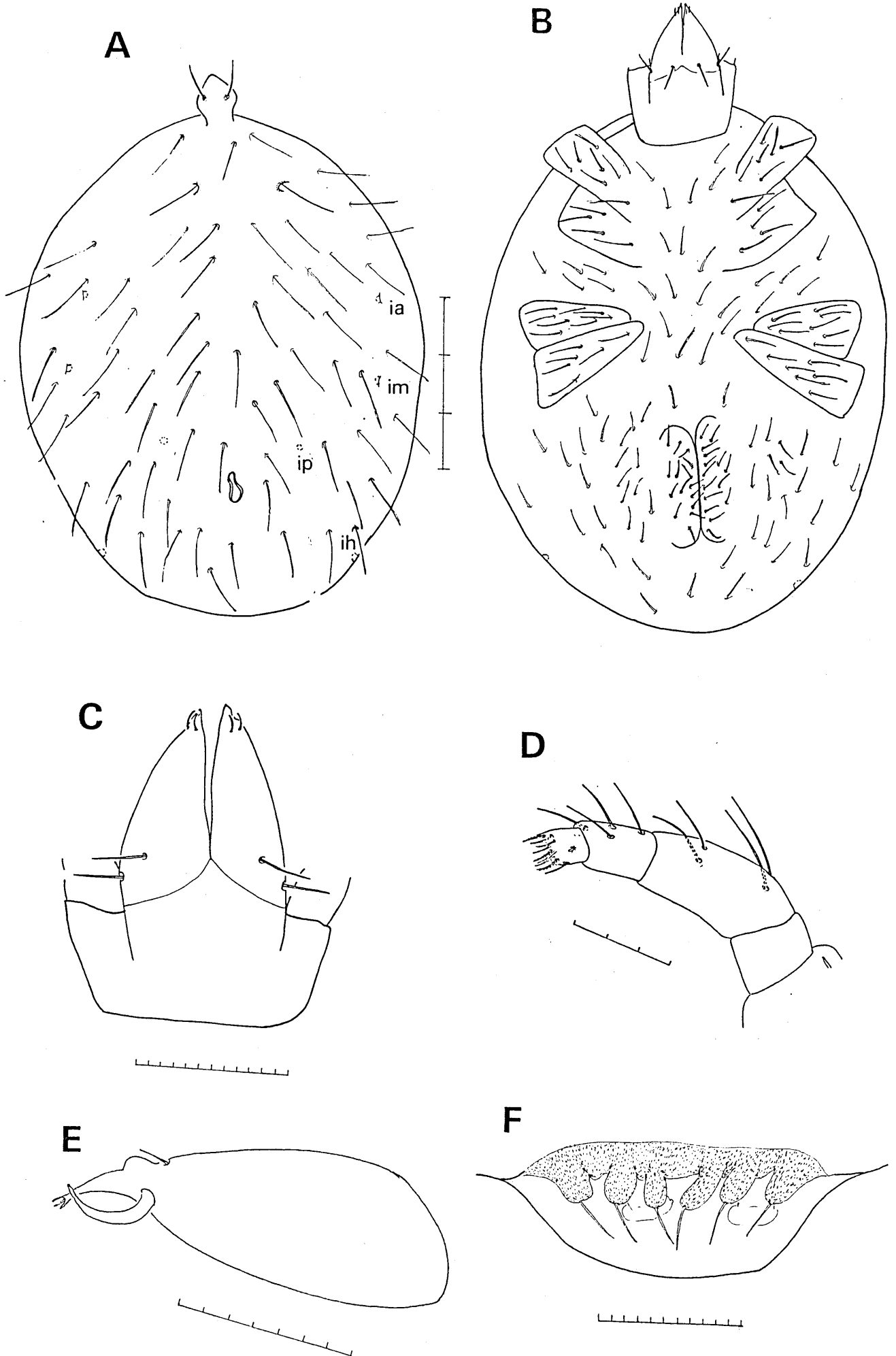


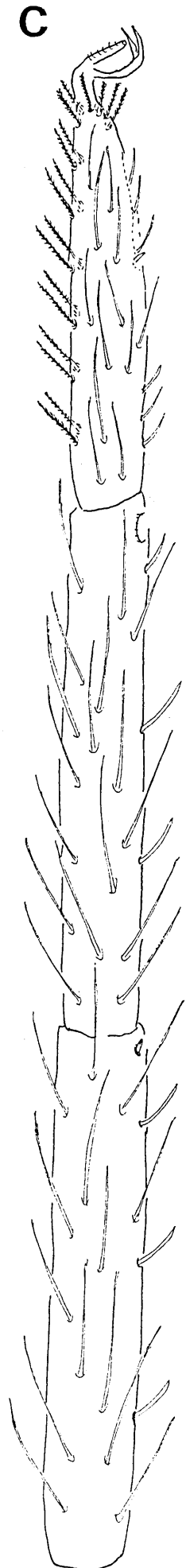
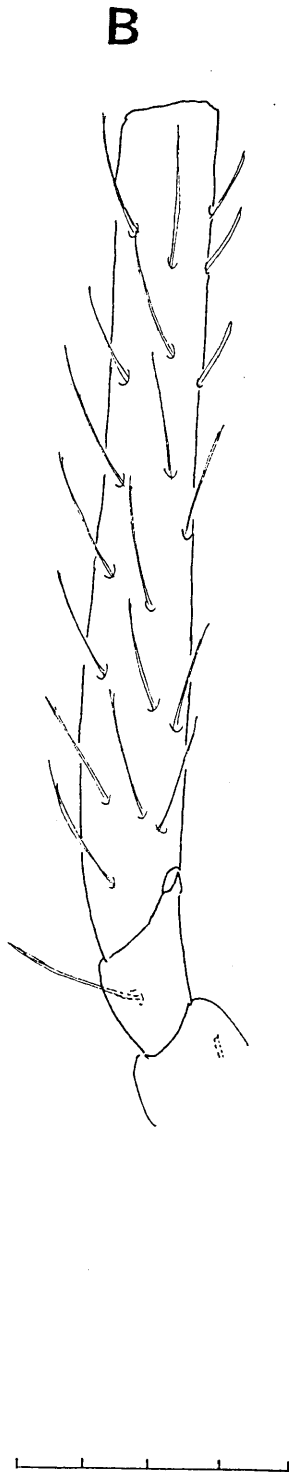
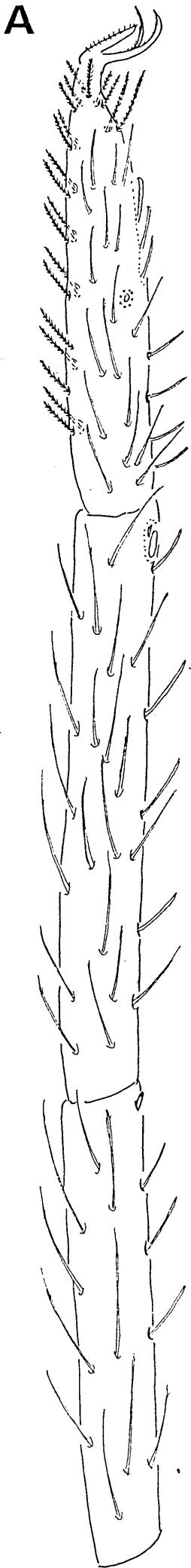
Fig. 97. *Penthaleus longipilis*:

(A) tarsus, tibia and genu I, posterolateral;

(B) femur and trochanter I;

(C) tarsus, tibia and genu II.

Scale intervals 10 μ m.



Penthaleus minor (Canestrini)

Figs 15d, 16a, 22c, 24a, 27a, 98 & 99

Notophallus minor Canestrini, 1886: 705.

DIAGNOSIS. *P. minor* can be distinguished from the other British species of the genus by its small size and relatively shorter setae.

Body length 420 (408-429), width 291 (283-299).

GNATHOSOMA (Figs 22c, 98B)

Subcapitulum: subcapitular setae subequal ca. 15 long.

Palp: setal formula 3-4-9.

Chelicera: total length 93 (89-96); *cha* ca. 7 long.

IDIOSOMA - DORSUM (Figs 15d, 16a, 98A)

Setae: strongly neutrichous, with respectively 15-18 and 37-43 prodorsal and opisthosomal setae; (*T*) ca. 25 long, remainder short, ca. 14 long, not overlapping each other.

IDIOSOMA - VENTER (Figs 24a, 98B)

Podosoma: setal number varies on either side of body and between specimens, ranges as follows - I 4, II 4-5, III 3-5, IV 3-5; 24-29 setae scattered between coxae; setae smooth, subequal ca. 12 long.

Genital area: six pairs smooth eugenital setae, ca. 13 long; 12-16 pairs genital setae, ca. 18 long, arranged in two longitudinal rows; 26 setae surrounding genital shields, not all forming pairs, smooth, ca. 20 long.

Anal region: anus surrounded by numerous smooth setae.

LEGS (Figs 27a, 99)

I and IV slightly shorter than body, II and III respectively just below and above two-thirds body length.

Setae: strongly neutrichous.

Solenidia: typical complement of semi-erect rhagidial organs; two or three erect solenidia on tibiae and genua, none discerned on tarsi or femora.

MALE. (3 specimens examined) (Fig. 98C) Sperm sac clavate, unornamented.

DISTRIBUTION. England, Italy, Wales.

MATERIAL EXAMINED. ITALY, Padova, R. Orto Botanica, 1891 [ISZA, slide no. 46/14] **British material:** ENGLAND, London, Clapham South, Rodenhurst Road, from cushion of moss on window ledge, ii.1982.

OTHER BRITISH RECORDS. ENGLAND, Cumbria, Ambleside, from rock face, 29.xi.1964 (M E Bacchus); Devon, near Cornwood, Higher Piles Copse (oak wood), from moss mat, mostly *Hypnum cupressiforme*, from surface of jumbled boulders in wood, 6.vi.1982 (P D Hillyard); Kent, Canterbury Nature Reserve, banks covered predominantly with *Phragmites* by power substation, from layer of moss amongst grass, 17.iii.1981. WALES, Dyfed, 1km north of Tregaron, Cors Tregaron, from moss at base of wall along nature reserve, 24.ii.1981.

REMARKS. I have applied the name *P. minor* for the same reasons given for utilizing *P. longipilis* (see **REMARKS**, p. 451).

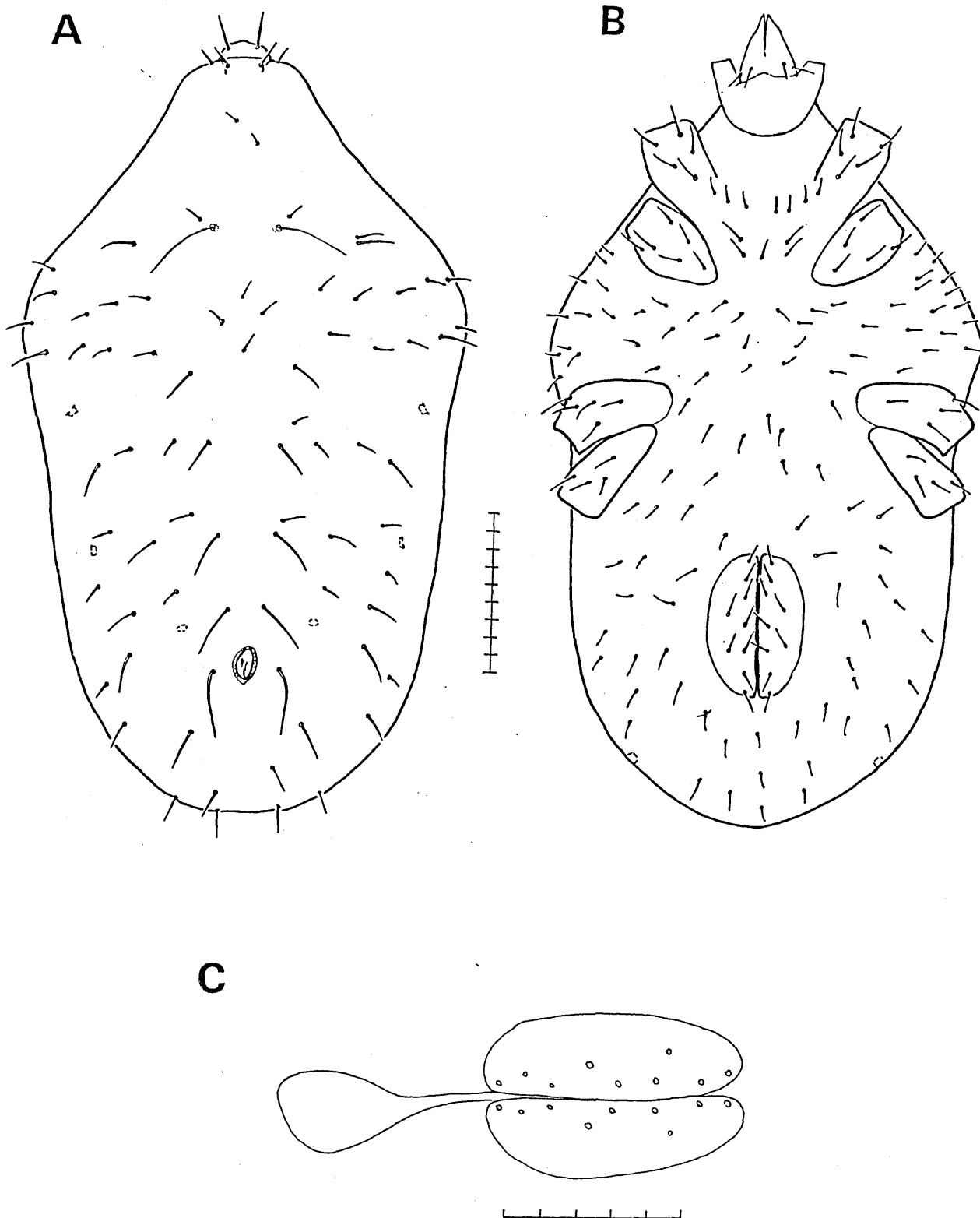


Fig. 98. *Penthaleus minor*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area ♂, sperm sac viewed through venter.

Scale intervals 10 μ m.

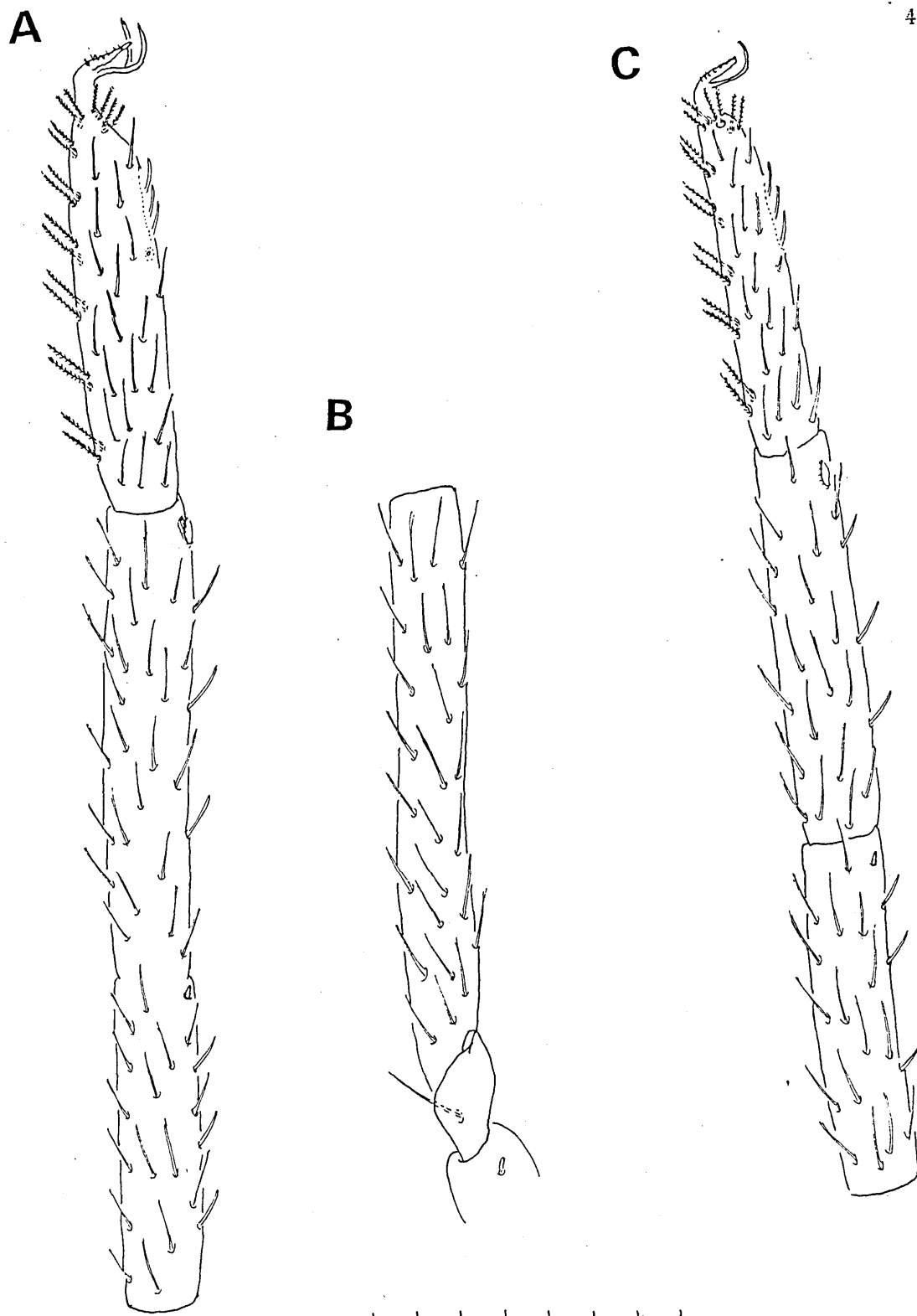


Fig. 99. *Penthaleus minor*:

(A) tarsus, tibia and genu I, posterolateral;

(B) femur and trochanter I;

(C) tarsus, tibia and genu II.

Scale intervals 10 μ m.

10.1.3 Family Penthalodidae Thor

Penthalodidae Thor, 1933: 57. Thor & Willmann, 1941: 57. Baker & Wharton, 1952: 177. Wainstein, 1978: 112. Strandtmann, 1971: 89; Kethley, 1982: 121.

DIAGNOSIS. Can immediately be distinguished from other eupodoid families by the presence of a prominent epirostrum associated with the naso and raised prodorsal eyes.

DEFINITION.

Small to medium (300-850 long), well-sclerotized.

Integument: idiosoma conspicuously ornamented, usually with reticulations, tubercles or punctations; prodorsal shield sometimes present; dorsally, V- to Y-shaped or two longitudinal furrows; appendages spiculate or papillate.

Chaetome: holo- or hypotrichous, sometimes neotrichous in genital area.

GNATHOSOMA.

Subcapitulum: spinose subcapitular setae of similar form; (*sbc*₁) inserted midway along subcapitulum, (*sbc*₂) approximately three-quarters of distance from (*sbc*₁) to anterior limit of subcapitulum; two pairs minute adoral setae.

Palps: long, slender without supracoxal seta; femur and genu longer than broad; tibiotarsus long, slender with small antiaxial rhagidial organ; setal formula 2-3-9; 1' spiralled.

Chelicerae with slender shaft; chela weakly chelate, edentate, account for at most one fifth of total length; *cha* apparently smooth, inserted slightly antiaxially, just proximal to chela, sometimes absent.

IDIOSOMA - DORSUM

Sejugal furrow either represented by line of differentiated integument subdividing idiosoma into prodorsum and opisthosoma or absent and idiosoma inverted pear-shape.

Naso: dome-like, delimited from prodorsum, with differentiated integument.

Epirostrum: more or less tri-lobed structure anterior to naso and extending partly over gnathosoma.

Eyes: conspicuous, raised dome-like, with differentiated integument.

Setae: (*iv*) much shorter and finer than others, apparently smooth, located on naso; (*T*) filiform, spiculated; (*c₂*) sometimes occupies anterior position approximately level with (*T*); if hypotrichous, *h* row absent.

Lyrifissures slit-like, margins heavily sclerotized.

IDIOSOMA - VENTER

Podosoma: coxae defined at distal limits only, heavily so; three or four setae on III, three on IV.

Genital area: shields roughly rectangular, all margins clearly delimited; genital setae mostly located along free edge of shields, one or two sometimes located slightly lateral to others; ovipositor an evagination of the eugenital area; sperm sac clavate, unornamented.

Anal region: anus subterminal, rarely dorsal, slit-like bounded by two flaps; three pairs pseudanal setae; (*lh*) lateral and slightly anterior to (*ps₃*).

LEGS.

I without supracoxal seta; usually all shorter than body length; all segments slender; distal papilla present on all genua.

Solenidia & famuli: tarsi I and II typically with three rhagidial organs, rarely, I with only two; rhagidial organs L-shaped, sometimes semi-erect;

famuli never elaborately developed; famulus present on tibia I; erect solenidia frequently occur on other segments.

Apotela: all of similar form.

TYPE GENUS. *Penthalodes* Murray

DISTRIBUTION. Cosmopolitan.

Genera classified in the family Penthalodidae

Penthalodes Murray 1877

Stereotydeus Berlese 1901

Key to the genera of the family Penthalodidae

1. With V- or Y-shaped furrow on idiodorsum, sejugal furrow absent

Penthalodes

- Idiodorsum without such markings, opisthodorsum with two parallel

longitudinal furrows, sejugal furrow present

* *Stereotydeus*

* Genus not recorded from the British fauna

10.1.3.1 Genus *Penthalodes* Murray

Penthalodes Murray, 1877: 123. Thor & Willmann 1941: 59. Strandtmann 1971: 91.

DIAGNOSIS. *Penthalodes* can be distinguished from the other penthalodid genus by the absence of the sejugal furrow and the V- or Y-shaped furrow idiodorsally.

DEFINITION

Small to medium (300-600).

Integument: with spiculated striae or with reticulate patterning formed by spicules; finely spiculated striae over V- or Y-shaped furrow; appendages spiculated.

Idiosomal form: inverted pear-shaped, often narrowly rounded posteriorly.

Chaetome: hypotrichous idiodorsally, setae of *h* row being absent; some localized neotrichy ventrally.

GNATHOSOMA

Subcapitulum: ratio length to width *ca.* 1:0.5; subcapitular setae spinose, subequal.

Palp: with long slender tibiotarsus, approximately three times greatest width.

Chelicera: chela reduced, accounting for approximately tenth of total length; fixed digit slightly forked distally; movable digit tapering in distal half; *cha* absent.

IDIOSOMA - DORSUM

Sejugal furrow: absent.

Epirostrum: prominent, tri-lobed, lateral lobes sometimes curved ventrally and inconspicuous.

Setae: (*iv*), (*ev*), (*sc*), (*c₁*), (*d₁*) and (*e₁*) all located within arms of dorsal furrow; (*ev*) lateral to and just posterior to naso; (*sc*) lateral to and approximately halfway between (*T*) and (*ev*); (*c₂*) markedly anterior to (*c₁*) in line with (*T*); (*h*) row absent; (*T*) short compared with most eupodoids; other setae plumose terminating in one to three long fine filaments.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-3-3; setae simple, spinose.

Genital area: seven pairs spiculated, simple eugenital setae; genital and aggenital simple, spinose; aggenital region sometimes neutrichous, setae forming two rows anteriorly.

Anal region: anus subterminal; (*ps₁*) just dorsal.

LEGS.

I just below body length.

Setae: spinose to plumose.

Solenidia & famuli: three rhagidial organs on tarsi I and II, one dorsodistally on tibiae I and II; tarsi with both recumbent and semi-erect rhagidial solenidia; famuli small, inconspicuous, variously located; erect solenidia on all tibiae and genua.

TYPE SPECIES. *Megamerus ovalis* Dugès

DISTRIBUTION. Northern hemisphere.

REMARKS. In spite of the cursory original description of the type species, *M. ovalis*, the figure given clearly indicates that the current concept of the genus conforms to that proposed by Murray (1877).

P. ovalis was the only member of the genus that had previously been recorded from the British Isles (Turk 1953).

Specific diagnoses refer only to the British species since the identity of most others was not clarified during the course of this study.

Key to the British species of *Penthalodes*

1. Small, idiosomal length around 400; posterior margin of opisthosoma rounded *P. ovalis*
- Large, idiosomal length around 550; posterior margin of opisthosoma pointed *P. nitidus*

Penthalodes ovalis (Dugès)

Figs 14c, 15a,e, 16d, 19a,c,e,f, 23c, 25d, 100 & 101

Megamerus ovalis Dugès, 1834: 50.*Penthalodes ovalis*: Thor & Willmann, 1941: 60; Strandtmann, 1971: 92.

DIAGNOSIS. *P. ovalis* can be distinguished by its small size and broadly rounded posterior margin of the opisthosoma.

Body length 378 (349-394), width 205 (194-211).

GNATHOSOMA (Figs 23c, 100B,C,D)

Subcapitulum: subcapitular setae ca. 7 long; (*sbc*₂) located approximately three-quarters distance from (*sbc*₁) and anterior limit of subcapitulum.

Palp: typical for genus.

Chelicera: total length 67 (64-71).

IDIOSOMA - DORSUM (Figs 14c, 15a,e, 16d, 100A)

Integument: spiculated, larger spicules form reticulate pattern, over Y spiculate-striate.

Setae: lengths - (*iv*) 4, (*T*) 49 (46-53), remainder increase gradually in length posteriorly from ca. 14-25.

IDIOSOMA - VENTER (Figs 25d, 100B,E)

Podosoma: setae subequal, ca. 20 long.

Genital area: eugenital setae, ca. 16 long; 10 pairs genital setae, ca. 14 long, (*g*₅) more lateral to others; six to ten pairs aggenital setae, ca. 18 long.

Anal region: (*ps*₁) at ca. 24, approximately one third longer than (*ps*₂ & 3).

LEGS. (Fig. 19a,c,e,f, 101)

I and IV just below body length, II and III respectively just over and just below two-thirds body length.

Setae: formulae I 1-9(4+5)-5-7-23, II 1-9(4+5)-5-6-15,

III 1-8(4+4)-4-6-15, IV 1-4(2+2)-5-6-15.

Solenidia & famuli: tarsi I and II with two semi-erect rhagidial organs between tectal setae plus one rhagidial organ just posteriorly, famuli posterolateral to base of recumbent organ, in separate pits; one dorsal erect solenidion distally on tibia I, genua I and II, medially on tibiae II and III, genua III and IV and proximally on tibia IV.

DISTRIBUTION. Alaska, England, Wales.

MATERIAL EXAMINED. WALES, Dyfed, 1km north of Tregaron, Cors Tregaron, from crevices in wall along nature reserve, 24.ii.1981.

OTHER BRITISH RECORDS. ENGLAND, Cumbria, Ambleside, from rock face, 29.xi.1954 (M.E. Bacchus).

REMARKS. This was an uncommon species found only from the above localities. The specific name is utilized, despite the absence of type material and the brief original description, since the specimens examined conform to other authors' concepts of the species.

Fig. 100. *Penthalodes ovalis*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) chelicera, antiaxial;

(D) palp, antiaxial, with tibiotarsus enlarged;

(E) genital area, ♀, lateral.

Scale intervals 10µm.

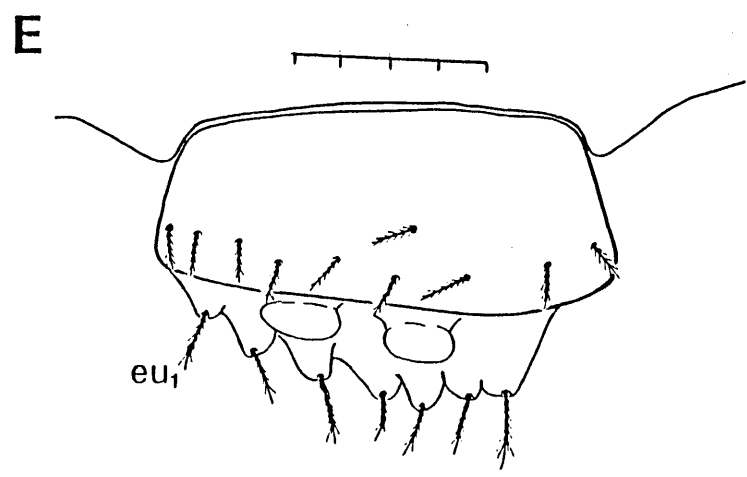
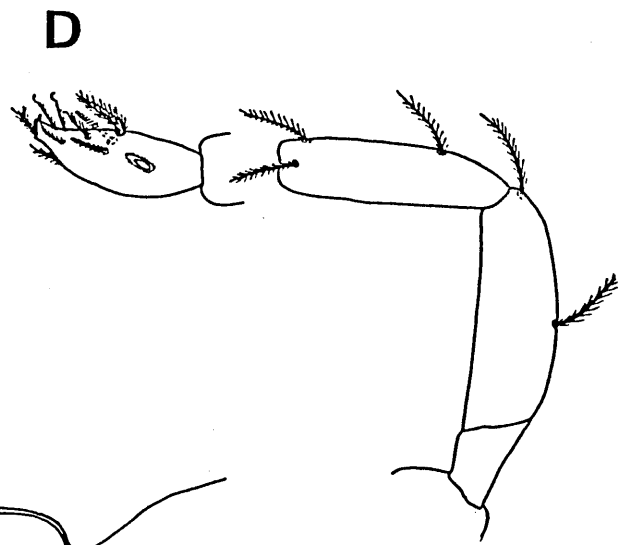
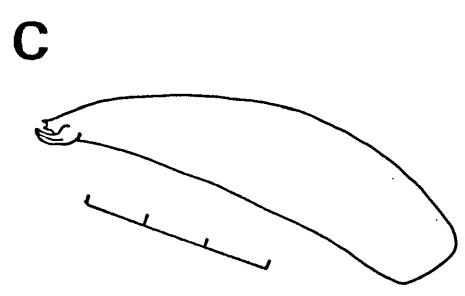
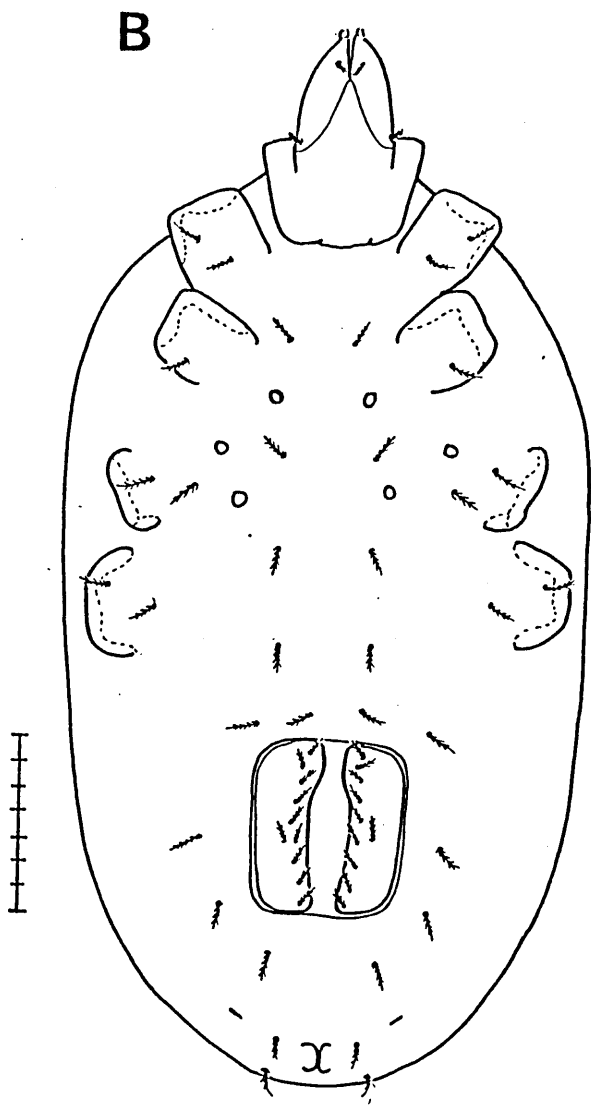
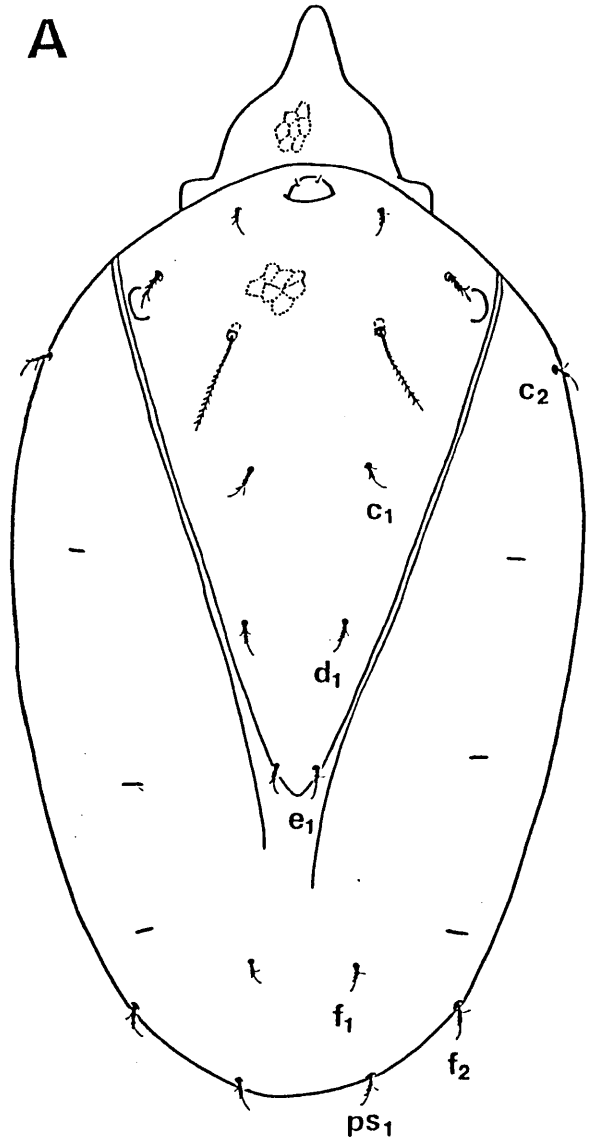
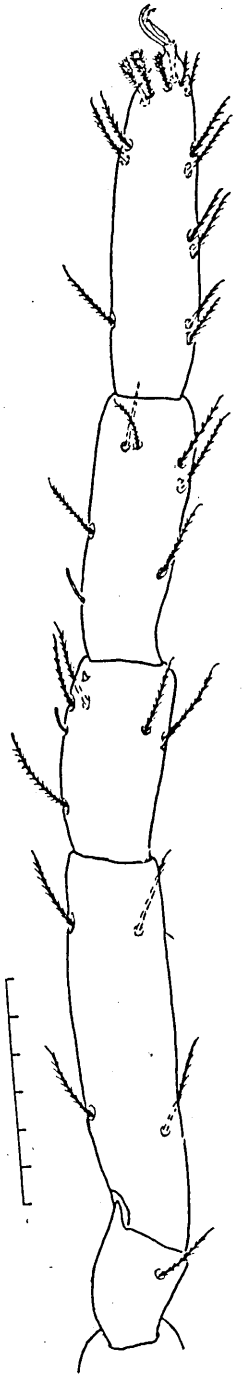
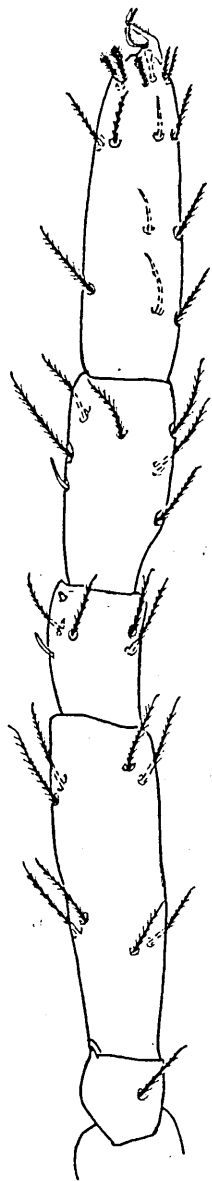
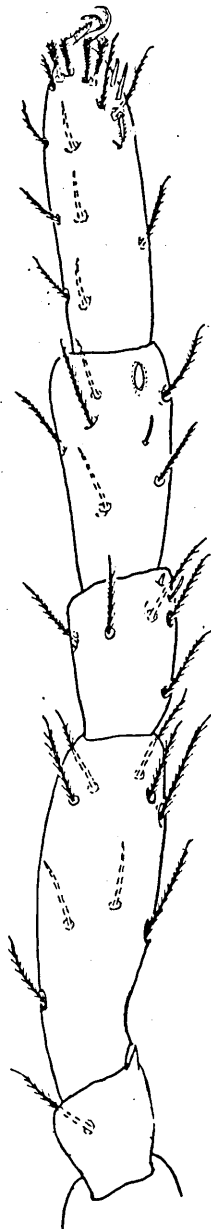
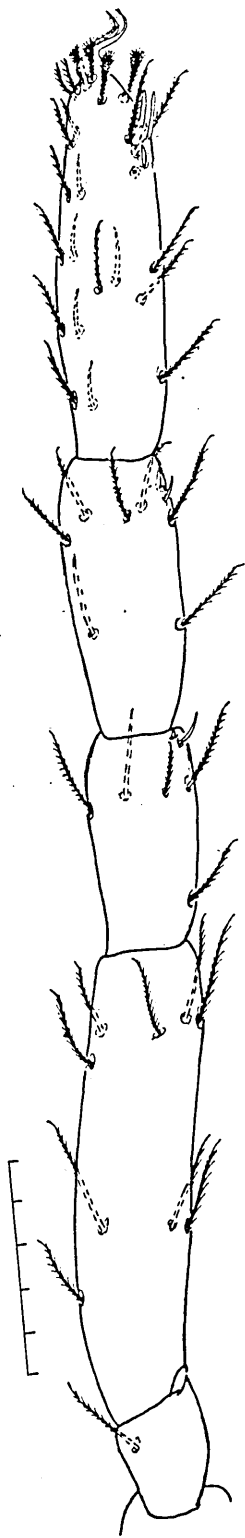
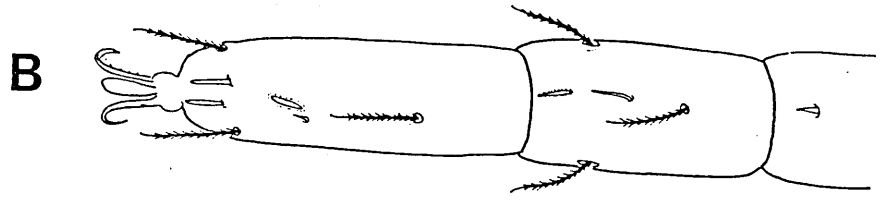
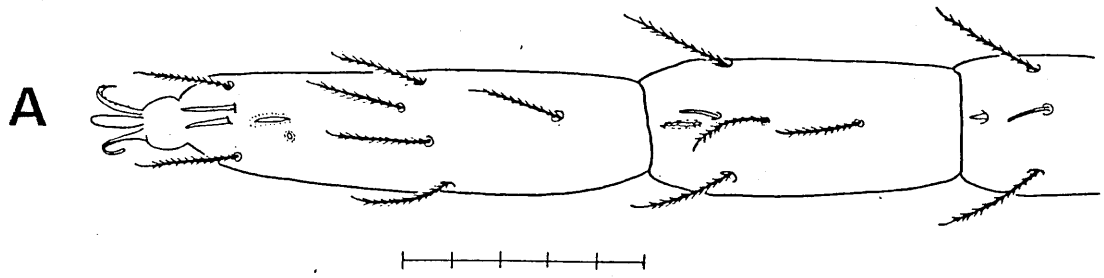


Fig. 101. *Penthalodes ovalis*:

- (A) leg I, dorsum of tarsus, tibia and distal part of genu;
- (B) leg II, dorsum of tarsus, tibia and distal part of genu;
- (C) leg I, posterolateral;
- (D) leg II, posterolateral;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



C

D

E

F

Penthalodes nitidus (Berles)

Figs 102 & 103

Chromotydaeus nitidus Berlese, 1920: 192.

DIAGNOSIS. *P. nitidus* can be distinguished from the other British species of the genus by its larger size and the narrowly pointed posterior limit of the opisthosoma.

Body length 550 (535-571), width 396 (387-403).

GNATHOSOMA (Fig. 102B)

Subcapitulum: subcapitular setae ca. 15 long; (*sbc*₂) located approximately three-quarters distance from (*sbc*₁) and anterior limit of subcapitulum.

Palp: typical for genus.

Chelicera: total length 125 (117-134); chela account for approximately one tenth of this.

DORSUM (Fig. 102A)

Integument: indented 'Y' formed from weakly spiculated striations, remainder of integument heavily spiculated, larger ones forming reticulations.

Epirostrum: with three peaks, the outer two much smaller than central one.

Setae: lengths - (*iv*) 4, (*T*) 58 (53-62), remainder ca. 28-33.

VENTER (Fig. 102B)

Podosoma: setae subequal ca. 31 long.

Genital area: eugenital setae increase in length posteriorly from ca. 13 to 18; nine pairs genital setae, ca. 12 long, (*g*₅) more lateral to others; approximately 12 pairs aggenital setae, six of which arranged in two rows

anteriorly to genital plates, from ca. 19 to 23 long.

Anal region: (ps_1 & ps_2) subequal, at ca. 25 approximately one quarter longer than (ps_3).

LEGS (Fig. 103)

I and IV slightly shorter than body, II and III respectively just over and just below two-thirds body length.

Setae: formulae - I 1-11(6+5)-6-11-23, II 1-9(4+5)-5-7-18,

III 1-8(4+4)-5-8-17, IV 1-4(2+2)-5-8-17.

Solenidia: tarsi I and II both with two semi-erect rhagidial organs between the tectal setae plus third small posterolateral rhagidial organ posteriorly; famuli just posterior and posterolateral to rhagidial organ; tibiae I and II both with erect solenidion subtending rhagidial organ; erect solenidion dorsoproximally on tibiae III and IV and dorsodistally on genua I to IV.

MALE. Unknown.

DISTRIBUTION. England, Italy

MATERIAL EXAMINED. Type material: La Plata (Bruck) [ISZA, slide no. 195/49]. ENGLAND, Devon, Appledore, from crevices in rocks at top of shore by life-boat house, 10.xii.1981.

REMARKS. This species was only found from the above locality.

Fig. 102. *Penthalodes nitidus*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) genital area, ♀, lateral.

Scale intervals 10 μ m.

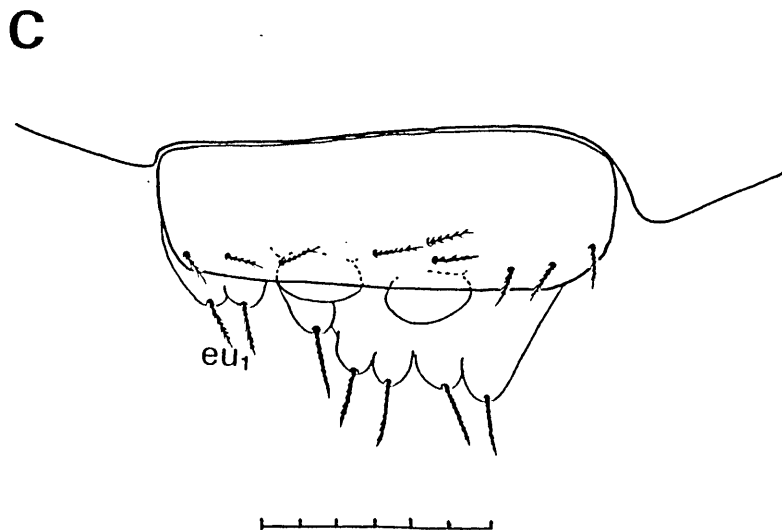
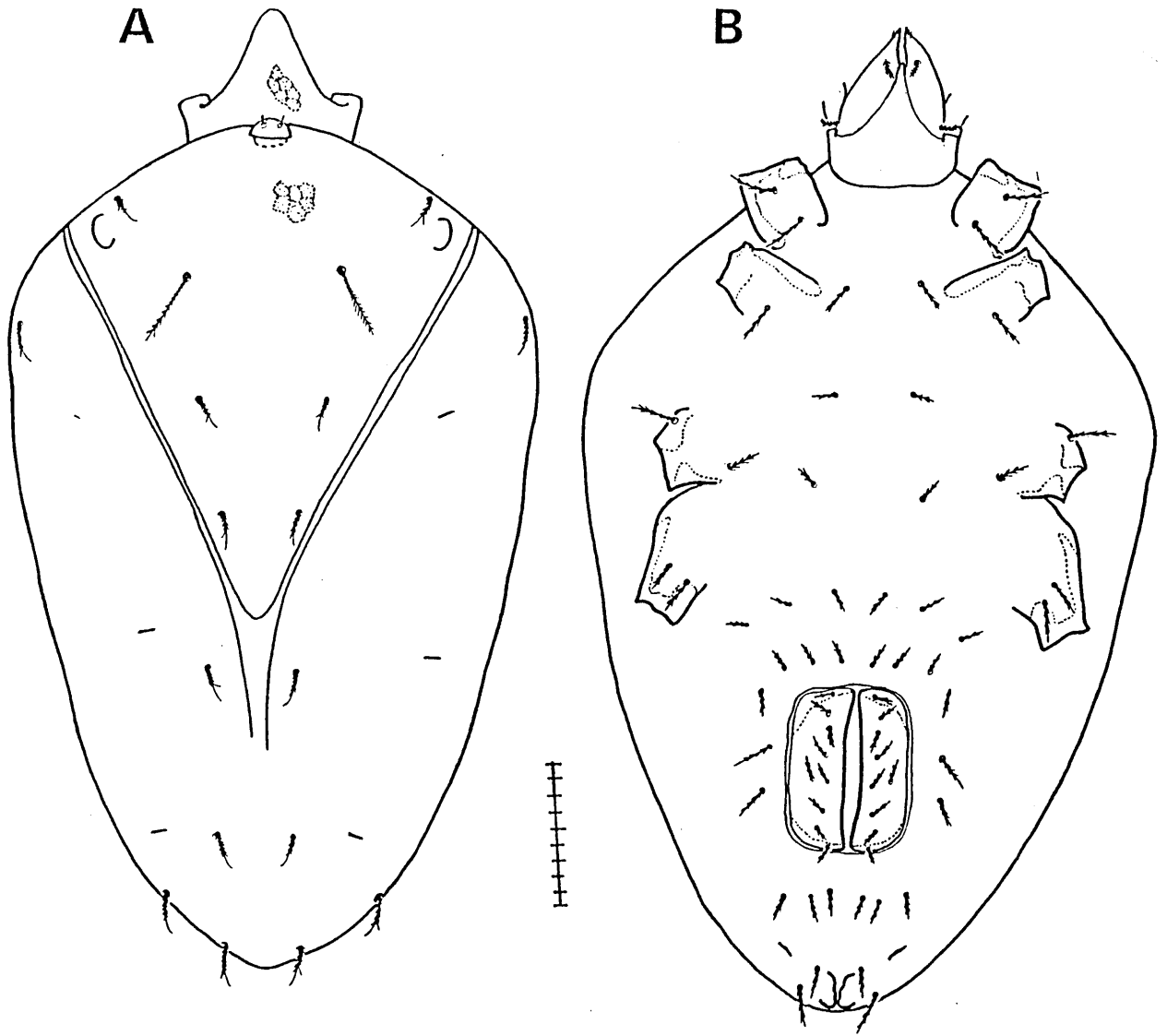
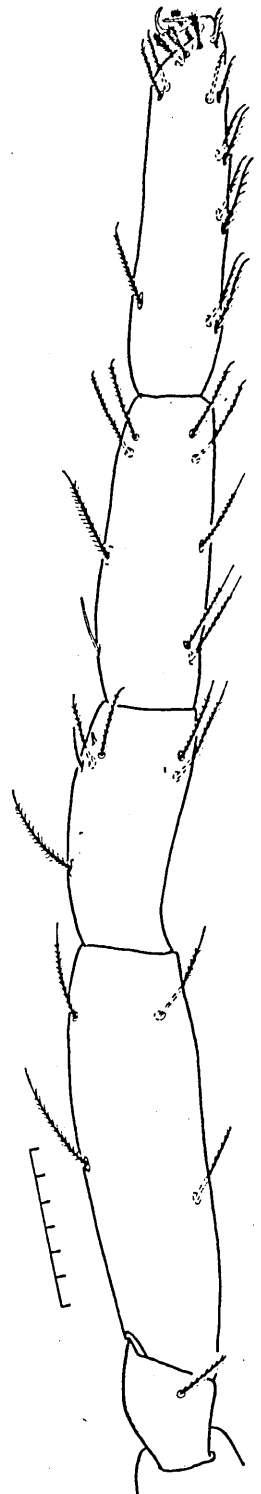
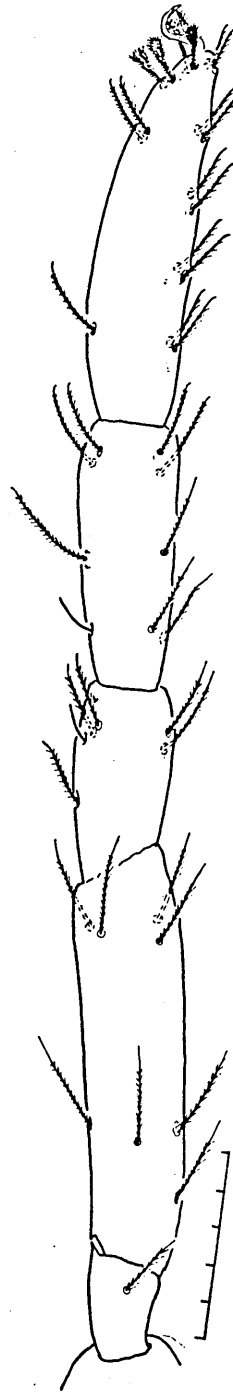
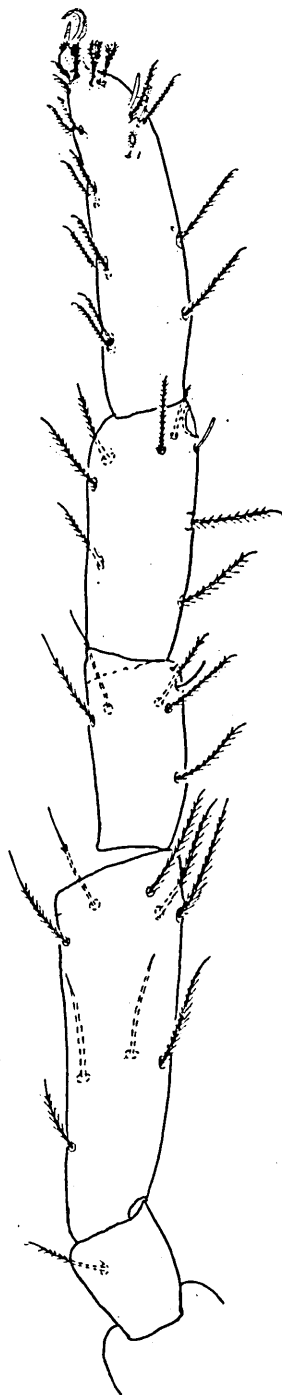
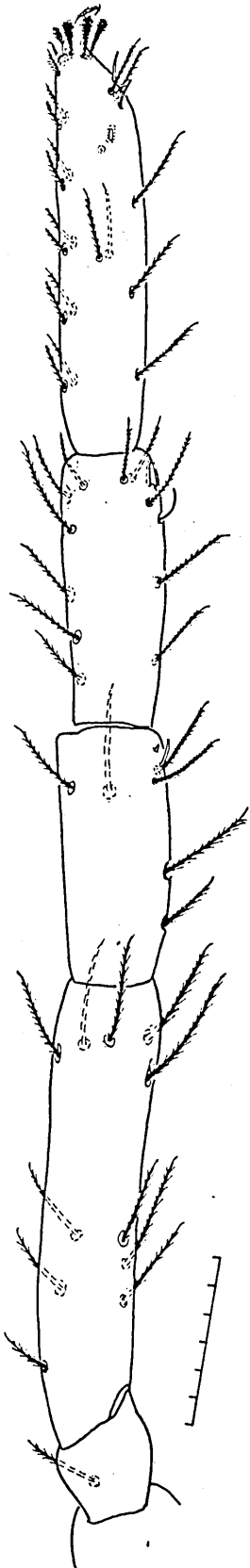
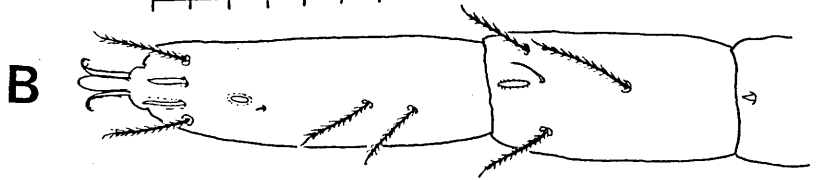
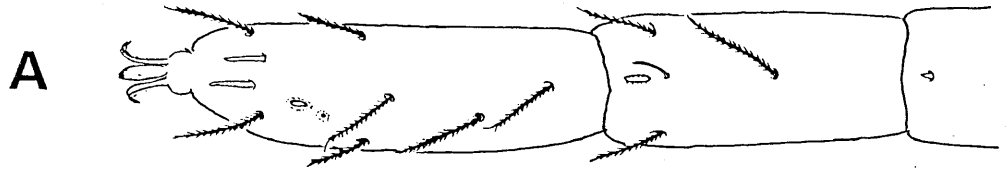


Fig. 103. *Fenthalodes nitidus*:

- (A) leg I, dorsum of tarsus, tibia and distal part of genu;
- (B) leg II, dorsum of tarsus, tibia and distal part of genu;
- (C) leg I, posterolateral;
- (D) leg II, posterolateral;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



C

D

E

F

10.1.4 Family Rhagidiidae Oudemans

Rhagidiidae Oudemans, 1922: 83. Thor & Willmann, 1941: 91. Baker & Wharton, 1952: 181. Strandtmann, 1971: 92. Wainstein, 1978: 110. Zacharda, 1980: 520. Kethley, 1982: 121.

Strandtmanniidae Zacharda, 1979: 77. Kethley, 1982: 122.

DIAGNOSIS. Distinguished from the other eupodoid families by the possession of robust, strongly chelate chelicerae, long adoral setae and one pair of adanal setae.

DEFINITION.

Small to large (270-2000 long), lightly sclerotized.

Integument: idiosoma weakly striate-spiculate, prodorsal shield with more densely spiculated striae; appendages spiculate or papillate.

Chaetome: usually holotrichous, rarely hypotrichous and (f_{22}) absent, one genus strongly neotrichous, localized neotrichy occurs in some species.

GNATHOSOMA

Subcapitulum: subequal, densely spiculated subcapitular setae located at approximately same level, halfway along subcapitulum; adoral setae long, easily discernible, rarely (or_1) absent; lateral lips usually divided into internal and external malae of varying form.

Palp: supracoxal seta short, apparently unornamented; genual length approximately equal to width, much shorter than tibiotarsus and femur; tibiotarsus up to five times longer than broad, broadly rounded distally, rarely slightly tapering; setae usually homeomorphic, densely spiculated, sometimes heteromorphic with some smooth; femur with two, occasionally one, setae, genu with three, rarely one or two; tibiotarsus with nine, 10

or 14 setae, solenidion dorsal and spiniform, occasionally rhagidiform, sometimes absent.

Chelicera: robust; chela strongly chelate, edentate, serrate or dentate, account for one quarter to one half total length; *cha* and *chb*, both smooth, normally present although, occasionally, only *cha* occurs, *cha* located dorsally on or just proximal to fixed digit, *chb* inserted slightly antiaxially on fixed digit.

IDIOSOMA - DORSUM

Sejugal furrow: divides body into roughly rectangular prodorsum and opisthosoma with prominent shoulders tapering to narrowly rounded posterior.

Naso varies from small to conspicuous rounded triangular extension of prodorsum, with or without a delimiting suture.

Eyes sometimes visible as subcuticular granular areas.

Setae: (*iv*) always located on naso; (*ev*) and (*sc*) approximately level with (*T*); *c* row always in line, (*f₂*) sometimes posterior and just lateral to (*f₁*); (*T*) filiform to capitate, spiculated; remainder spinose or densely spiculated or spinose.

Lyrifissures round.

IDIOSOMA - VENTER

Podosoma: coxae normally completely and distinctly defined, respective pairs, especially I and II, almost meet medially; setae spatulate, blunt, spinose or densely spiculated; coxa III with four to six setae, IV with three, rarely, four.

Genital area: densely spiculated, tapering eugenital setae mounted on tubercles, never heteromorphic; genital shields roughly semi-circular, outer margins indistinct; densely spinose genital setae always in single file; ovipositor with whorls of eugenital setae; sperm sac clavate, unornamented.

Anal region: anus slit-like, terminal, visible in dorsal view; three pairs pseudanal setae, (ps_1) dorsal, (ps_2) subterminal, (ps_3) ventral; one pair adanal setae located on anal flaps, often much shorter than pseudanals; (ih) located laterally and just anteriorly to (ps_3).

LEGS

Slender, although tarsus I sometimes slightly inflated; leg I usually longer than body.

Setae: short to long; densely spiculated or spinose, normally simple, rarely prorals of tarsus II-IV capitate.

Solenidia & famuli: variously arranged; rhagidial organs L-, T- or inverted U-shaped; three or more rhagidial organs on tarsus I, usually three or more on tarsus II, rarely only two; tarsal famuli occasionally elaborate, that of II sometimes absent; one, rarely two or three, rhagidial organ distally on tibiae I and II, that of II subcuticular; famulus of tibia I absent; rhagidial organs sometimes also occur on tibiae III and IV, genu I to III and tarsus III; erect solenidia mostly spiniform, sometimes long and blunt, usually present on tibiae I-IV and genua I-III, rarely occur on certain tarsi and femora.

Apotela: usually of similar form with slender, tapering empodium, in one genus apotele I greatly expanded; rarely, empodium with terminal clawlet.

TYPE GENUS. *Rhagidia* Thorell

DISTRIBUTION. Cosmopolitan.

Genera classified in the family Rhagidiidae

Rhagidia Thorell 1871

Coccorhagidia Thor 1934

Latoempodia Zacharda 1980

Pilorhagidia Strandtmann & Goff 1978

Shibaia Zacharda 1980

Troglocheles Zacharda 1980

Key to the genera of the family Rhagidiidae

- | | |
|---|-----------------------|
| 1. (T) clavate or capitate | 2 |
| - (T) simple | 3 |
| 2. dorsal idiosomal chaetome neutrichous; 3 setae on trochanter IV | |
| * <i>Pilorhagidia</i> | |
| - dorsal idiosomal chaetome holotrichous; two setae on trochanter IV | |
| <i>Coccorhagidia</i> | |
| 3. proral setae of tarsi II-IV capitate; with six or more rhagidial organs on tarsus I | † <i>Troglocheles</i> |
| - proral setae all simple; with four or less rhagidial organs on tarsus I | 4 |
| 4. rhagidial organs of tarsus I arranged level and parallel to longitudinal axis of segment; famulus distal to all rhagidial organs | <i>Shibaia</i> |
| - rhagidial organs of tarsus I not arranged as above; famulus never distal to all rhagidial organs | 5 |
| 5. apotele I greatly enlarged | <i>Latoempodia</i> |
| - apotele I same form as II-IV. | <i>Rhagidia</i> |

† see REMARKS on genus *Rhagidia* (section 10.1.4.1)

10.1.4.1 Genus *Rhagidia* Thorell

Rhagidia Thorell, 1871: 700. Thor & Willmann, 1941: 96. Strandtmann, 1971: 101.

DIAGNOSIS. Can be distinguished from the other genera of the family by the combination of filiform trichobothria, famulus I never distal to all rhagidial organs, tarsal setae simple and apotela all of similar form.

DEFINITION.

Small to large (430-2000).

Chaetome: holotrichous, some localized neotrichy.

GNATHOSOMA.

Subcapitulum: internal and external malae normally clearly differentiated, acuminate or membranous; two pairs adoral setae.

Palp: femur and genu can both be deficient in one seta, tibiotarsus usually with 10 setae but nine and 14 also occur; spiniform solenidion normally present, although sometimes not discernible or slightly recessed.

Chelicera: chela from third to quarter of total length, of variable form; fixed digit sometimes terminates in a number of small cusps; inner margin of movable digit smooth, dentate or serrated; *chb* rarely, absent; *cha* located just proximal to or at base of fixed digit, *chb* sometimes inserted in pit or on small tubercle.

IDIOSOMA - DORSUM

Naso: small to large rounded triangular extension of the prodorsum.

Setae: (7) filiform, rarely somewhat thickened, spiculated particularly in distal two-thirds; remainder densely spiculated simple, approximately quarter to half intersetal distance.

Lyrifissures: as for family.

IDIOSOMA - VENTER

Podosoma: coxae I and II with respectively three and one setae, III from four to nine, IV from three to eight; setae densely spiculated, tapering to spatulate.

Genital area: up to 14 pairs eugenital setae; four to six pairs densely spiculated genital setae, tapering to spatulate; four to six pairs densely spiculated tapering to spatulate aggenital setae, neotrichy sometimes occurs in this area with as many as 12 pairs setae.

Anal region: as for family.

LEGS.

I from three-quarters to longer than body, II and III approximately half to three-quarters body length, IV three-quarters to just shorter than body.

Setae: generally long, densely spiculated.

Solenidia & famuli: rhagidial organs T- or L-shaped, variously arranged; tarsus I most commonly with four rhagidial organs, sometimes three or five, II normally with three, sometimes two or five organs; one, rarely two, organs on tibia I; spiniform solenidia present on most tibiae and genua; famuli never elaborate, variously located but never distal to rhagidial organs.

Apotele: all of similar form; clawlets sometimes present.

MALE. Sperm sac as for family.

TYPE SPECIES. *Rhagidia gelida* Thorell.

DISTRIBUTION. Cosmopolitan.

REMARKS. The membership of the genus *Rhagidia* has recently undergone much change due to the revision by Zacharda (1980) (see critique in section 9). Based on results of the systematic analyses carried out in this study, the majority of Zacharda's supra-specific taxa could not be supported and hence

Rhagidia, though a paraphyletic group in cladistic terms, is here returned to its original concept for ease of identification.

Thirteen species of *Rhagidia* have been recorded from the British Isles (Halbert 1915, Hull 1918, Evans 1952, Hazelton 1961, 1970, 1972, Wood 1967, Turk 1967, 1972). Of these, *R. spelaea* was collected during the present study, while *R. muscicola* Hull, *R. halophila* (Laboulbene), *R. longipes* Trägårdh, *R. vitzhumi* Turk, *R. intermedia* Willmann and *R. reflexa* Koch are now considered to be *species indeterminata*. Examples of the remaining five species *R. gigas* (Canestrini), *R. terricola* (Koch), *R. mucronata* Willmann, *R. saxonica* Willmann and *R. diversicolor* (Koch) were not available for study.

The figures in the description of *R. odontochela* Turk clearly show the capitate proral setae on tarsi II to IV that are diagnostic of the genus *Troglocheles* Zacharda (Turk 1972). Unfortunately, the type material is apparently lost, while no examples were found during the course of this study.

Key to the British species of the genus *Rhagidia*

- | | |
|--|------------------------|
| 1. (<i>T</i>) thickened; three rhagidial organs on tarsus I | <i>R. arena</i> |
| - (<i>T</i>) fine; four rhagidial organs on tarsus I | 2 |
| 2. five setae on coxa III; five genital setae; rhagidial organs of tarsus II obliquely parallel | <i>R. punkva</i> |
| - four or six setae on coxa III; five or six pairs of genital setae; rhagidial organs of tarsus II in tandem | 3 |
| 3. six pairs genital setae | <i>R. clavicrinita</i> |
| - five pairs genital setae | 4 |
| 4. six setae on coxa III; one dorsodistal rhagidial organ on tibia I | <i>R. spelaea</i> |
| - four setae on coxa III; two dorsodistal rhagidial organs on tibia I | <i>R. montana</i> |

Rhagidia arena Zacharda n.comb.

Figs 104 & 105

Poecilophysis (Soprocheles) arena Zacharda, 1980: 639.New British record

DIAGNOSIS. This species can be immediately distinguished from the other members of the genus by the presence of the long rhagidial organ on tarsus II subtending two adjacent minute organs and the thickened trichobothria.

Body length 462 (449-491), width 181 (170-188).

GNATHOSOMA (Figs 104C,D,E)

Subcapitulum: ratio length to width 1:0.45; internal malae needle-like, externals broad; two pairs adoral setae; subcapitular setae subequal, ca. 24.

Palp: setal formula 2-3-10; solenidion present, spiniform; tibiotarsal length approximately twice width.

Chelicera: total length 189 (180-197), chela accounting for just under half of this; *cha* 16 long, approximately half length of *chb*; both setae located on fixed digit, respectively one and two thirds distance from base; fixed digit rather slender, inner margin smooth, terminates in five small cusps; movable digit slightly more robust with serrated inner margin; small spine in angle of digits.

IDIOSOMA - DORSUM (Fig. 104A)

Naso: small peak.

Setae: (*T*) thickened; lengths - (*iv*) 22 (20-25), (*ev*) 29 (27-32),
 (*T*) 85 (82-89), (*sc*) 68 (65-71), (*c₁*) 26 (24-28), (*c₂*) 61 (58-65),
 (*d₁*) 23 (21-25), (*e₁*) 24 (22-27), (*f₁*) 60 (57-64), (*f₂*) 24 (21-26),
 (*h₁*) 57 (54-61), (*h₂*) 25 (22-27).

IDIOSOMA - VENTER (Fig. 104B)

Podosoma: setal formula 3-1-5-3; setae ca. 23-28 long.

Genital area: 10 pairs eugenital setae, subequal ca. 16 long; five pairs both genital and aggenital setae, respectively ca. 14 and 21 long.

Anal region: (*ps₁*), at 42 (39-44), approximately 2.5 times longer than (*ps₂*) and three times longer than (*ps₃*) and (*ad₁*).

LEGS. (Fig. 105)

I slightly shorter than body, II and III just over half body length, IV approximately three-quarters.

Setae: formulae I 1-10(5+5)-11-10-18, II 1-10(5+5)-7-7-15,
 III 2-8(4+4)-6-6-14, IV 2-(4+4)-6-6-16.

Solenidia & famuli: tarsus I with four rhagidial organs arranged obliquely parallel in distal half of segment, famulus located posterolaterally between proximal two; tarsus II with three rhagidial organs, proximal occupies approximately median third of segment, subtends two adjacent minute organs, famulus just posterolateral to base of proximal organ; tibia I and II with small distal rhagidial organ and associated erect solenidion just posteriorly; tibia III with one spine and one erect solenidia located adjacent to one another dorsoproximally; tibia IV with dorsoproximal erect solenidion; genua I and II with ventrodiscal spine; genu III with one median anterolateral spine.

MALE. Unknown.

DISTRIBUTION. Czechoslovakia, England.

MATERIAL EXAMINED. Type material: Holotype ♀ , CZECHOSLOVAKIA, Moravia mer., Valtice, 'Rendezvous', moss on sandy substratum, 14.iv.1974 (V. Bukva) [MZ]; paratype ♀ , same data as holotype. ENGLAND, Wiltshire, Savernake Forest, approximately 900m S of junction of paths, oak copse edged by hawthorn, from oak litter, 17.ix.1981; Suffolk, Hollesley Common, from litter and fermentation layer under pine, ii.1984.

OTHER BRITISH RECORDS. This was an uncommon species, only being found from the above samples.

Fig. 104. *Rhagidia arena*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) chelicera, antiaxial.
- (E) palp, antiaxial;

Scale intervals 10 μ m.

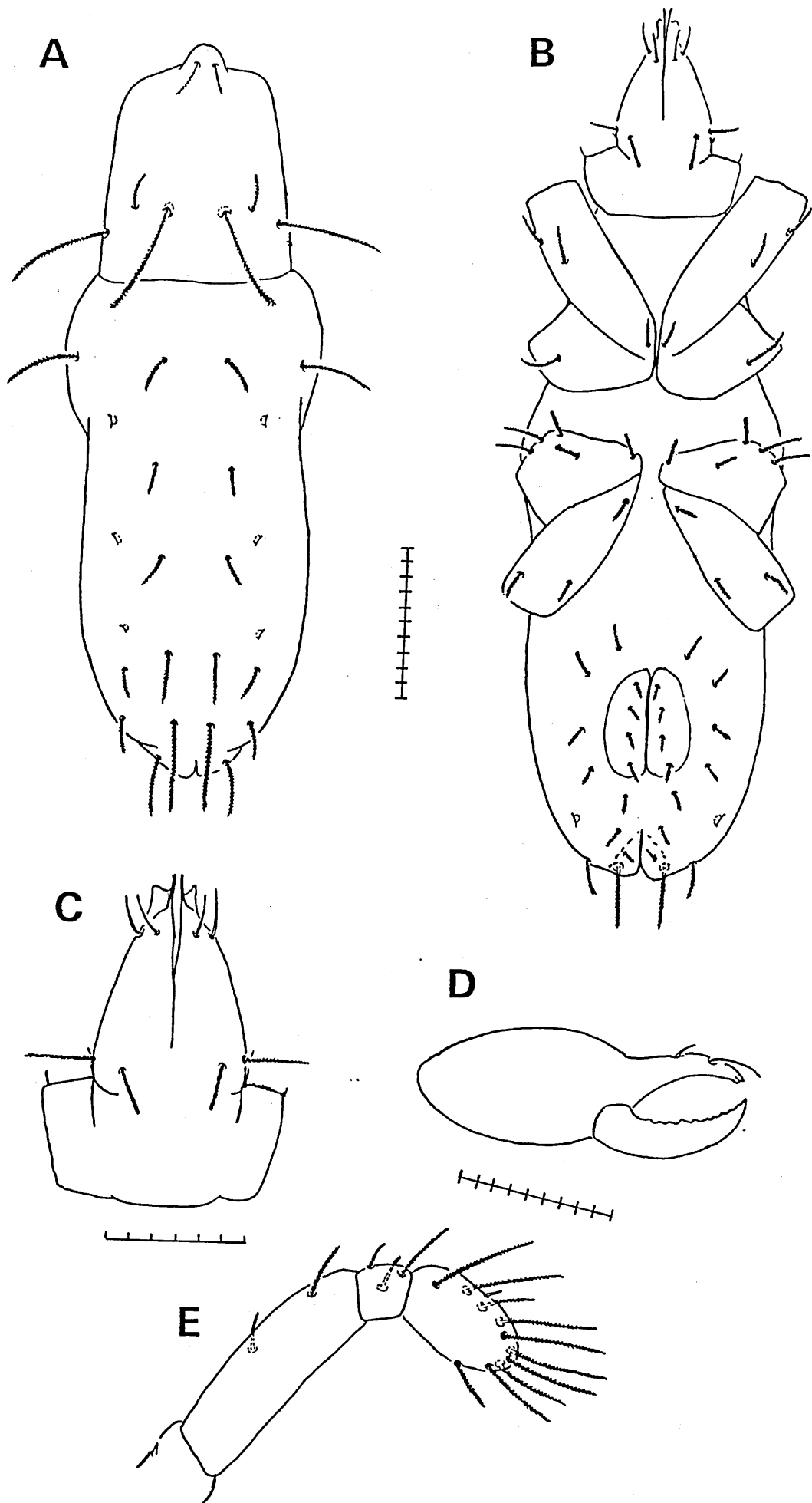
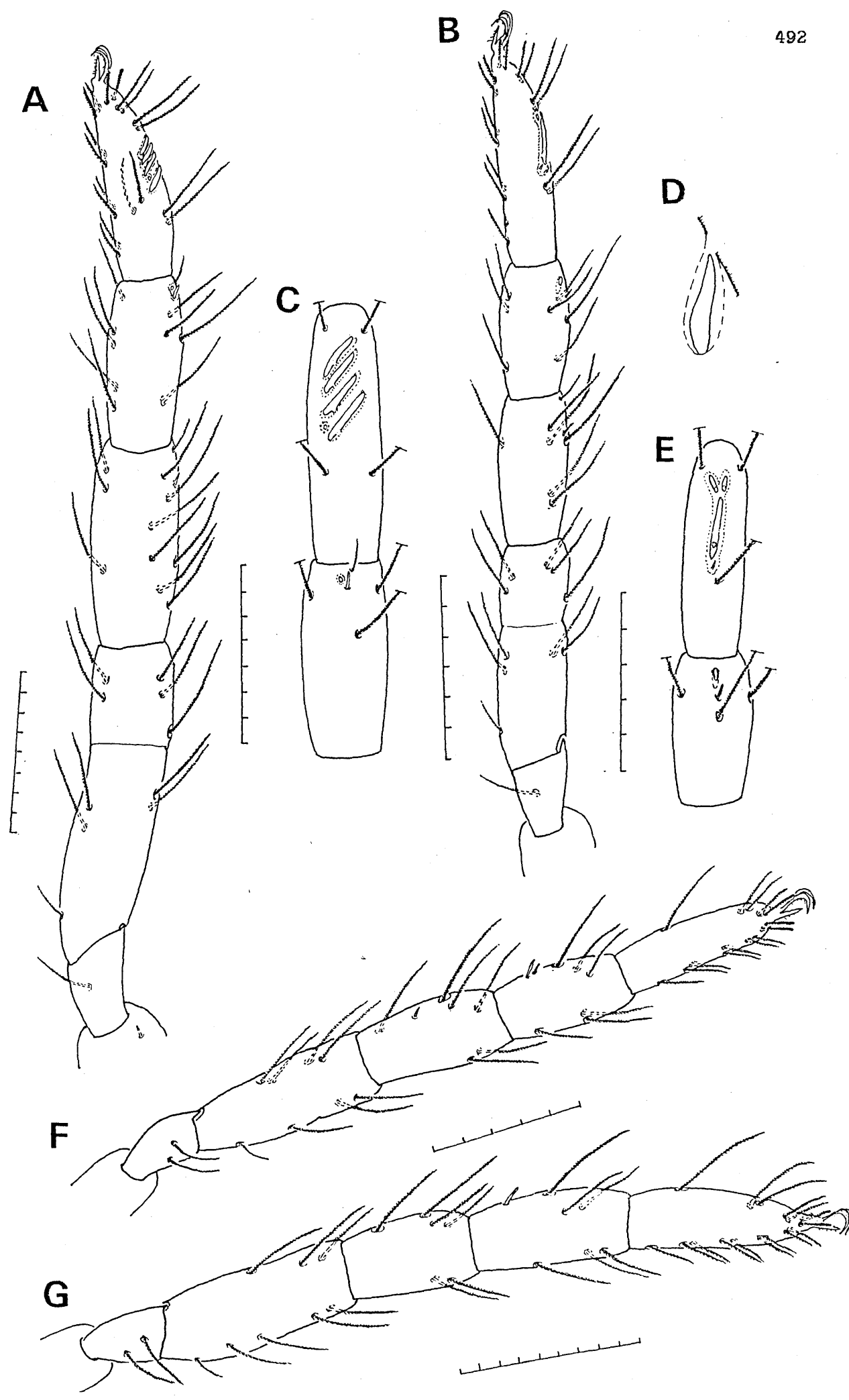


Fig. 105. *Rhagidia arena*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tibia II, subcuticular rhagidial organ, lateral;
- (E) tarsus & tibia II, dorsal;
- (F) leg III, anterolateral;
- (G) leg IV, anterolateral.

Scale intervals 10 μ m.



Rhagidia clavicrinita Ehrnsberger comb.rev.

Figs 106 & 107

Rhagidia clavicrinita Ehrnsberger, 1977: 95.*Foveacheles (Usitorhagidia) clavicrinita*: Zacharda, 1980: 685.New British record

DIAGNOSIS. Differs from all other species of the genus by possessing six pairs of genital setae, a striated antiaxial surface of the movable cheliceral digit and, respectively, four and three rhagidial organs on tarsi I and II, those of the latter being arranged in tandem.

Body length 763 (735-813), width 290 (273-312).

GNATHOSOMA (Figs 106C,D,E)

Subcapitulum: ratio length to width 1:0.5; internal malae needle-like, external malae membranous; two pairs adoral setae; subcapitular setae ca. 65 long.

Palp: setal formula 2-3-10; spiniform solenidion present; tibiotarsal length just over twice width.

Chelicera: total length 190 (185-201); chela account for third of length, robust, edentate; fixed digit without cusps; movable digit with antiaxial diagonal striations along basal third; *cha* located ca. one quarter of length from base of fixed digit, *chb* slightly antiaxial approximately midway between *cha* and end of digit; *cha* at 13 approximately half length of *chb*

IDIOSOMA - DORSUM (Fig. 106A)

Naso: clearly visible as rounded protrusion.

Setae: (*sc*), (*c₂*), (*f₁*) and (*h₁*) markedly longer than other setae, lengths - (*iv*) 65(61-69), (*ev*) 47(44-51), (*T*) 105(99-108), (*sc*) 121(117-135), (*c₁*) 44(41-47), (*c₂*) 125(119-127), (*d₁*) 39(37-41), (*e₁*) 42(39-44), (*f₁*) 90(86-95), (*f₂*) 45(42-49), (*h₁*) 119(115-123), (*h₂*) 46(39-49).

IDIOSOMA - VENTER (Fig. 106B,F)

Podosoma: setal formula 3-1-6-3.

Genital area: 10 pairs subequal, ca. 12 long, eugenital setae; six pairs subequal, 30 long, blunt genital setae; five pairs subequal, ca. 38 long, spatulate aggenital setae.

Anal region: (*ps₁*) ca. 100 long, twice length of other three pairs.

LEGS (Fig. 107)

I fifth longer than body, II and III respectively just under and over two-thirds, IV approximately equal to body length.

Setae: ventrals of tarsus and tibia I robust; formulae I 1-11(6+5)-11-10-21, II 1-10(5+5)-10-6-16, III 2-8(4+4)-5-6-14, IV 2-7(4+3)-5-6-12.

Solenidia & famuli: tarsus I with four dorsal obliquely parallel rhagidial organs in separate pits, famulus located posterolaterally between two proximal organs; tarsus II with three dorsal rhagidial organs, in tandem and in confluent pits, subtended by famulus; tibia I with dorsoproximal spine and small dorsal rhagidial organ near distal margin of segment; tibia II with one posterolateral spine proximally.

MALE. (2 specimens examined) (Fig. 106G). Sperm sac typical for family.

DISTRIBUTION. Czechoslovakia, Eire, England, Federal Republic of Germany.

MATERIAL EXAMINED. Type material: holotype ♂, FEDERAL REPUBLIC OF GERMANY, 2300 Kiel, beech forest litter, x.1969 (R. Ehrnsberger) [OU, slide no. 29617]. British material: EIRE, Co. Clare, Burren, from vegetation in limestone crack, 1.ix.1968 (M. E. Bacchus). ENGLAND, Lancashire, Boggle Crag, 500m north of Satterthwaite, from oak humus, 26.ix.1962 (P. N. & K. Lawrence)

OTHER BRITISH RECORDS. ENGLAND, Cambridgeshire, Woodwalton Fen, path along SW edge of Compartment 79 (pasture), from fresh mole-hill, 30.vi.1981; Kent, Chiddingstone, Chiddingstone Cave, from rotting oak leaves in threshold zone of cave, 1.ii.1981. Suffolk, Westleton Heath, 15km NE of Westleton, from litter layer of bracken with some *Polytrichum* moss at edge of heath, 9.i.1981; Yorkshire, Boltons Abbey, moss off stone wall of Abbey, ca. 10cm from ground, 20.ii.1982.

Fig. 106. *Rhagidia clavicrinita*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) subcapitulum, venter;

(D) chelicera, antiaxial;

(E) palp, antiaxial.

(F) genital area ♀, ovipositor extruded;

(G) genital area ♂, sperm sac viewed through venter.

Scale intervals 10µm.

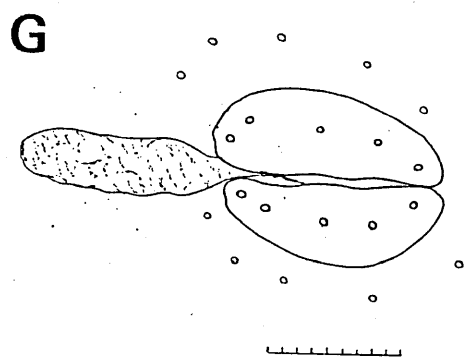
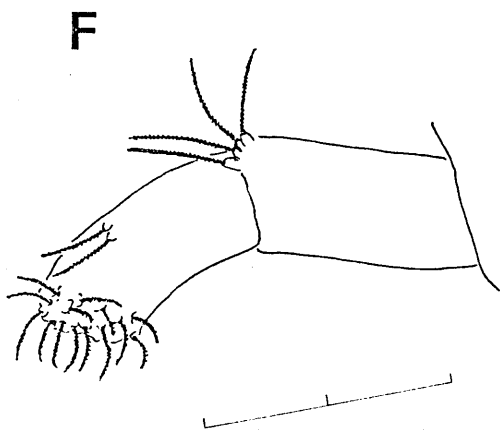
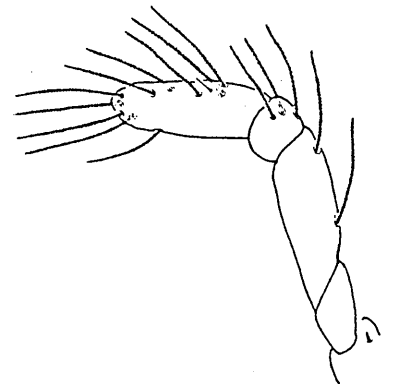
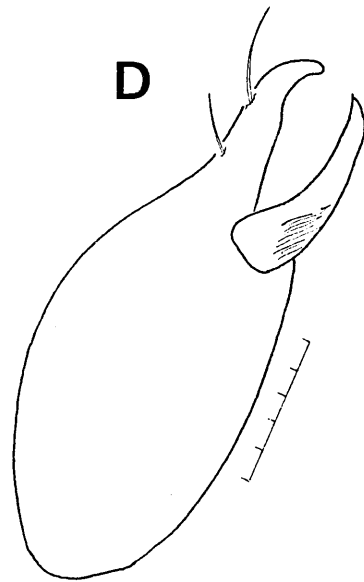
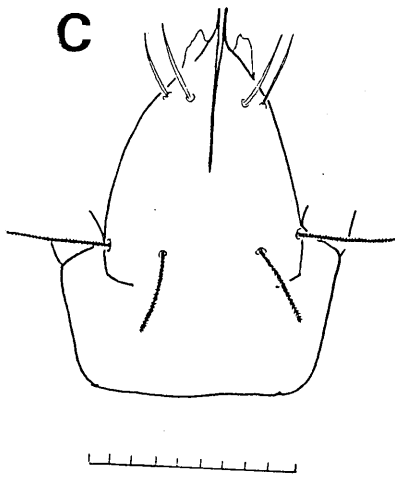
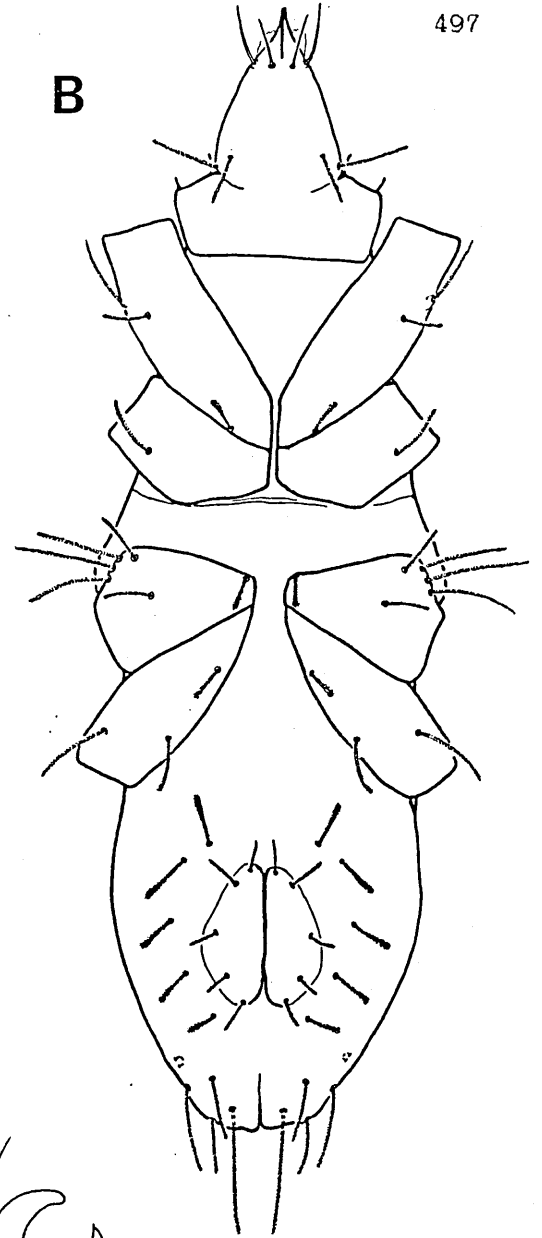
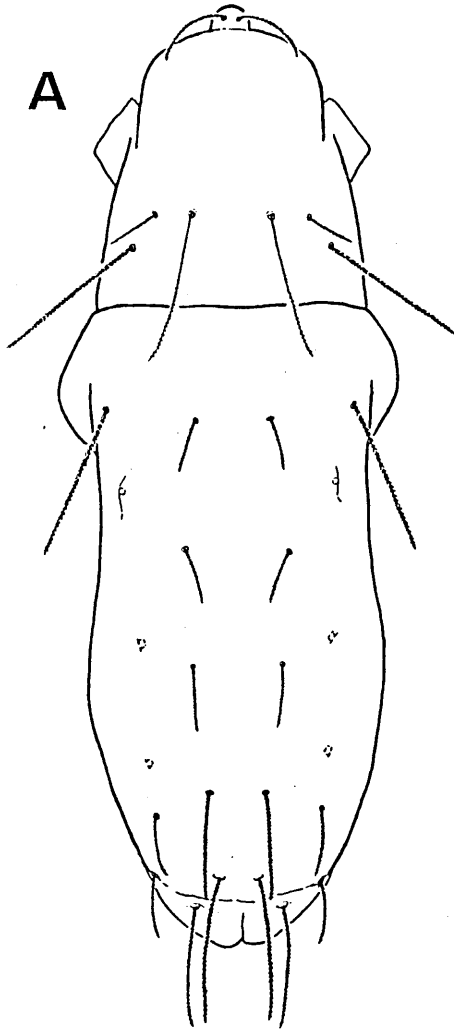
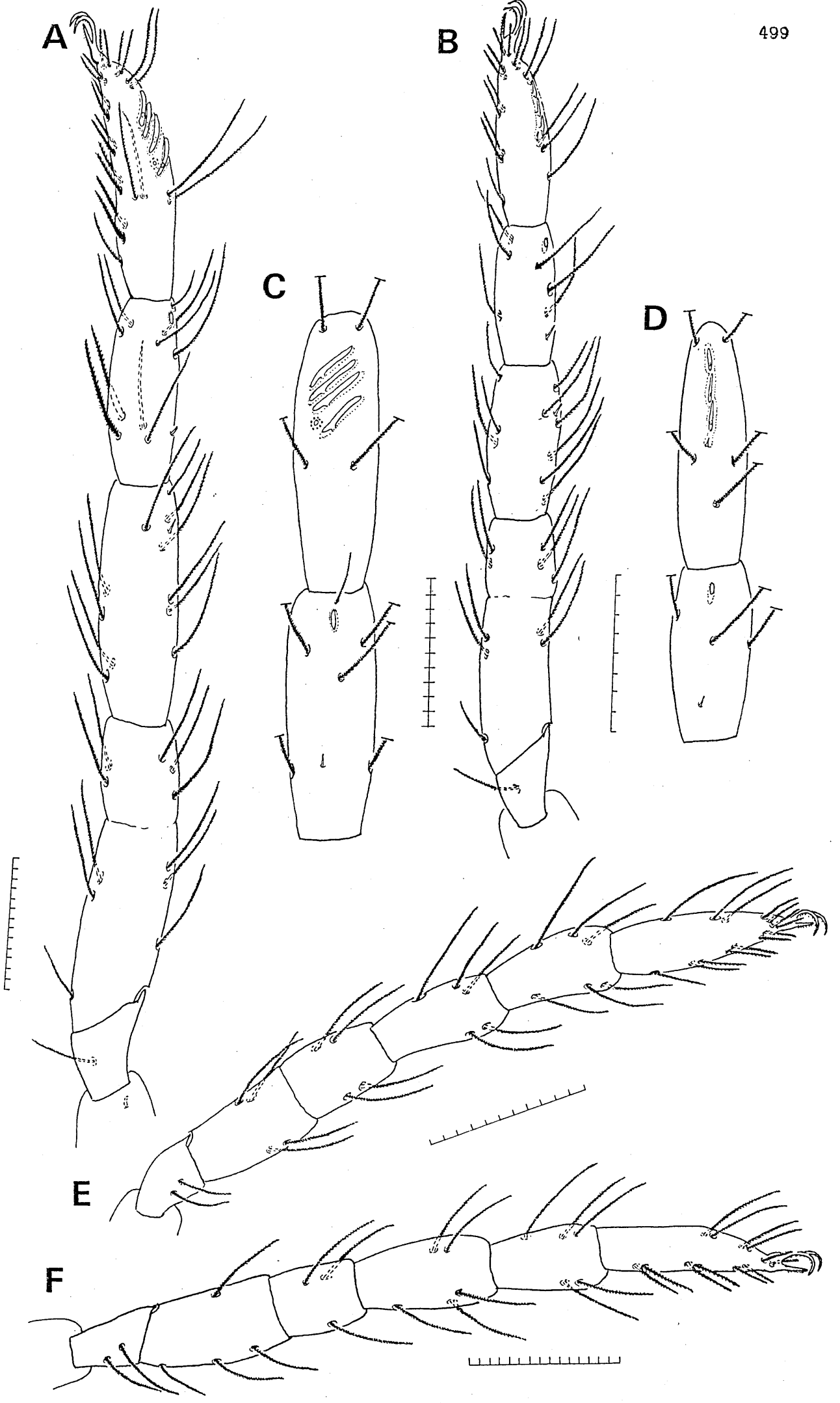


Fig. 107. *Rhagidia clavicornita*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Rhagidia montana (Zacharda) n.comb.

Figs 108 & 109

Robustocheles (*Robustocheles*) *montana* Zacharda 1980: 529.New British record

DIAGNOSIS. *R. montana* can be distinguished from other species of the genus by the robust fixed digit of the chelicera in combination with the presence of four setae on coxa III, five pairs of both genital and aggenital setae and two dorsodistal rhagidial organs on tibia I

Body length 690 (678-703), width 297 (291-302).

GNATHOSOMA (Figs 108C,D,E)

Subcapitulum: ratio length to width 1:0.4; internal malae long needle-like; external malae inconspicuous, acuminate; subcapitular setae ca. 40 long; two pairs adoral setae.

Palp: setal formula 2-3-10; solenidion present, spiniform; tibiotarsal length approximately 2.5 times width.

Chelicera: total length 220 (215-223), chela count for just over third of this; *cha* 20 (18-23), about half length of *chb*; setae located respectively third and two-thirds distance along fixed digit; fixed digit robust terminates in four small cusps, movable digit robust serrated along median third of inner margin.

IDIOSOMA - DORSUM (Fig. 108A)

Nasop: conspicuous roughly triangular extension of prodorsum.

Setae: lengths - (iv) 37(35-40), (ev) 33(31-35), (I) 82(78-86), (sc) 80(76-83), (c₁), (d₁), (e₁), (f₂), (h₂) subequal 32-34, (c₂) 58(55-62), (f₁) 51(48-53), (h₁) 60(57-65).

IDIOSOMA - VENTER (Fig. 108B)

Podosoma: setal formula 3-1-4-3; ca. 27.

Genital area: 8 pairs eugenital setae; subequal ca. 12 long; five pairs genital and aggenital setae, respectively ca. 12 and 15 long.

Anal region: (ps₁) 40(38-43) ca. respectively twice and three times length of (ps₂) and of (ps₃) and (ad₁).

LEGS. (Fig. 109)

I just over, IV just under three-quarters body length, II and III just over half body length.

Setae: formulae - I 1-11(6+5)-11-10-19, II 1-10(5+5)-8-7-16,

III 2-8(4+4)-6-5-14, IV 2-7(4+3)-6-6-14.

Solenidia & famuli: tarsus I with four rhagidial organs obliquely parallel in separate pits, famuli located posterolaterally between two proximal organs; tarsus II with three rhagidial organs slightly overlapping each other in tandem and contiguous pits, famulus subtending; tibia I with two small dorsodistal rhagidial organs in same pit; subcuticular rhagidial organ of tibia II with slit-like pore; one distal spiniform solenidion respectively posterolaterally and anterolaterally on genua I and II; one posterolateral spine proximally on tibiae II, IV and genu III; two proximal spines in tandem just posterolaterally on tibia III.

Apotela: all of similar form.

KALE. Unknown.

DISTRIBUTION. Czechoslovakia, England, German Federal Republic, Scotland, Wales.

MATERIAL EXAMINED. Type material: holotype ♀, CZECHOSLOVAKIA, Storakia, Velká-Tatra-Mountains, Cierny Kamen, litter and rhizosphere of grass, 18.vi.1974 (V. Bukva) [MZ]. British material: ENGLAND, Kent, The Warrens, Folkestone, 300m west along coast path, from thin covering of moss and grass, 17.iii.1981.

OTHER BRITISH RECORDS. ENGLAND, Hampshire, Alice Holt Forestry Commission, near Bentley, from pasture, 24.v.1965 (P.N. Lawrence); Leicestershire, 12km S of Hinckley, area of oak wood edged by hawthorn, from oak litter ca. 200m into wood; Suffolk, Dunnich Forest, Corsican pine (*Pinus nigra*) plantation bordered by oak trees, from mixed oak and pine litter layer, 9.i.1981. SCOTLAND, Grampian, Craigellachie, birch wood, from under stones amongst trees, 17.ix.1982. Highland, Tainish, by Tainish Cottage, from moss covering ground under beech, 14.ix.1982. WALES, Dyfed, 1.5km N of Tregaron, Cors Tregaron, West Bog, from moss (*Hypnum* sp.) and *Calluna* roots on dry ridge, 24.ii.1981; Borth, Ynysias Nature Reserve, mature sand dunes ca. 200m from top of beach, from mixed mosses plus underlying 1 cm of sandy soil, 25.ii.1981.

Fig. 108. *Rhagidia montana*:

- (A) idiosoma, dorsum;
 - (B) idiosoma, venter;
 - (C) subcapitulum, venter;
 - (D) chelicera, antiaxial.
 - (E) palp, antiaxial;
- Scale intervals 10 μ m.

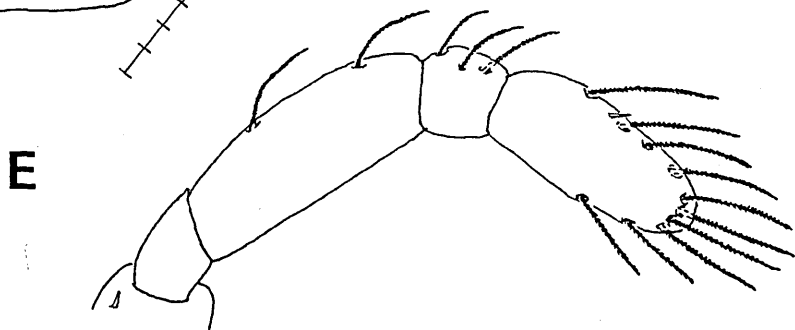
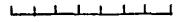
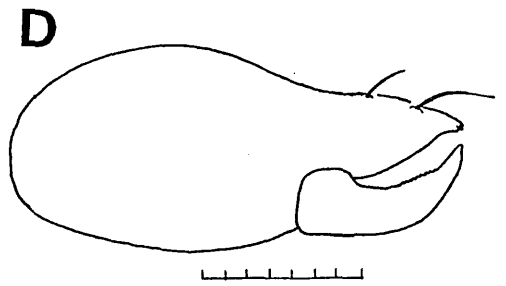
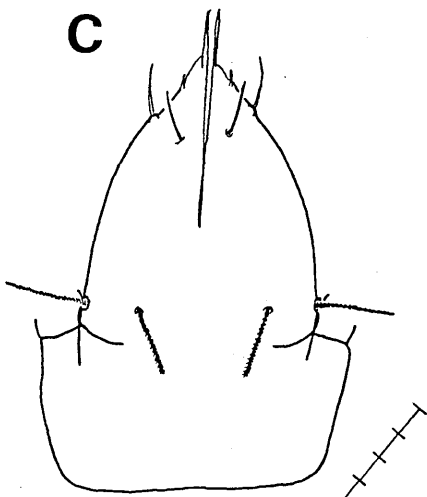
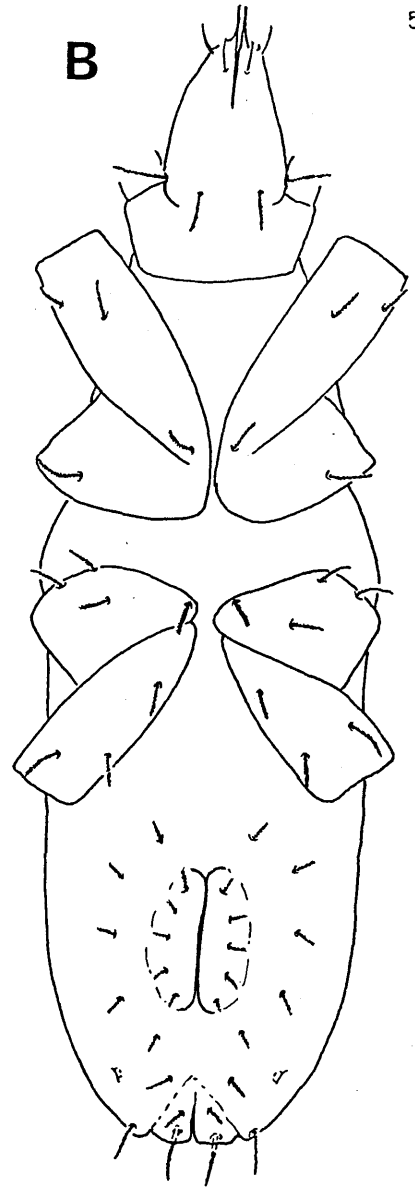
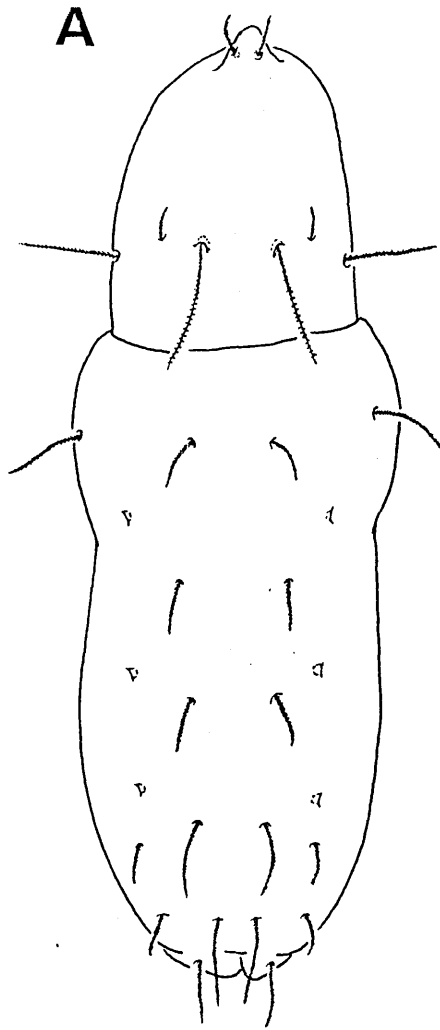
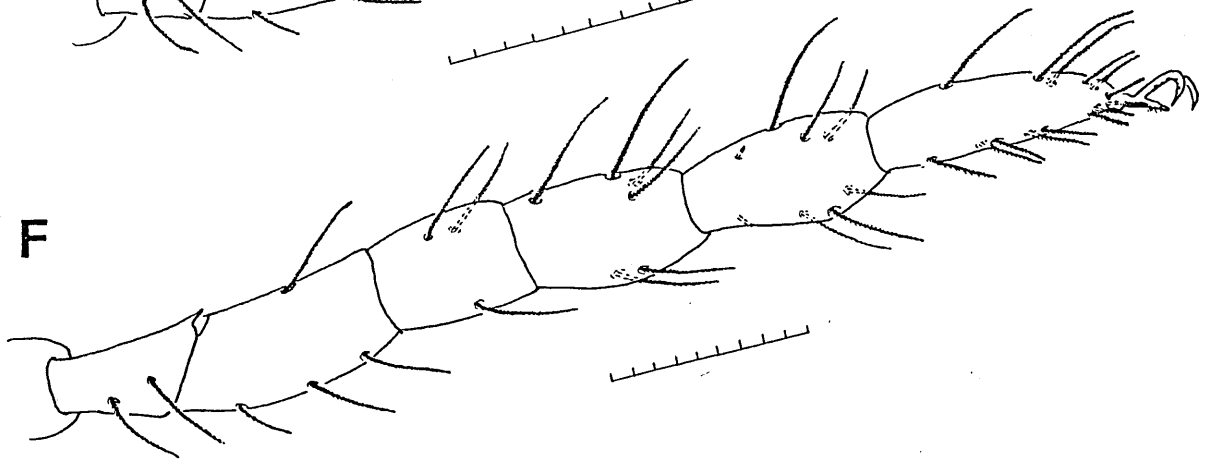
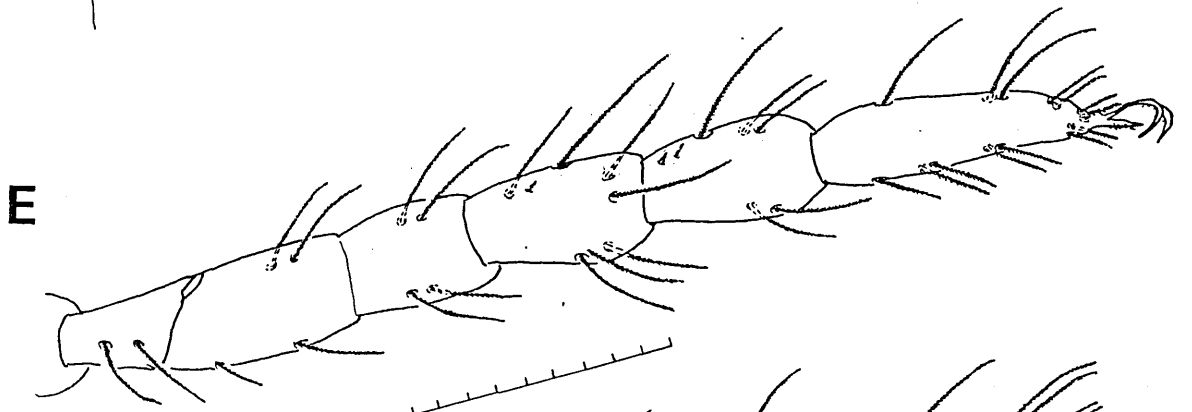
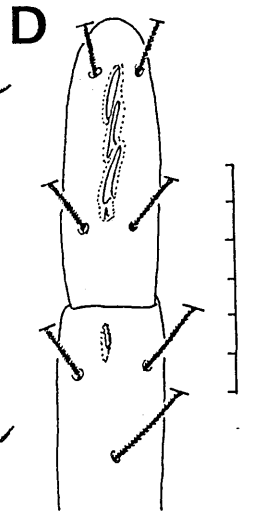
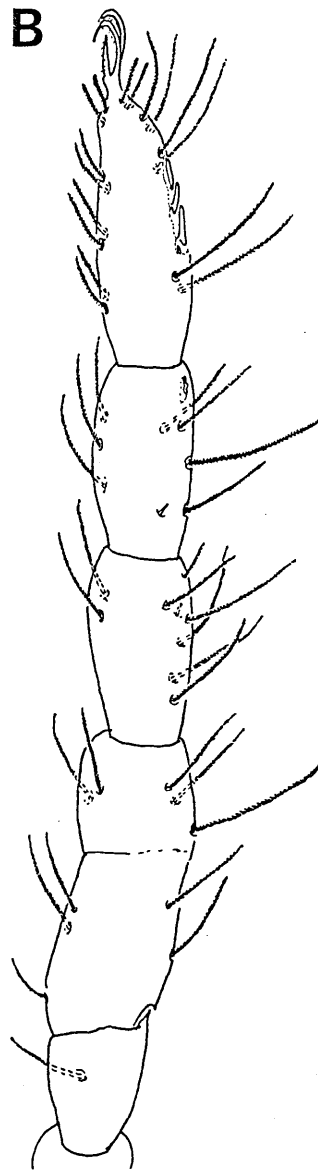
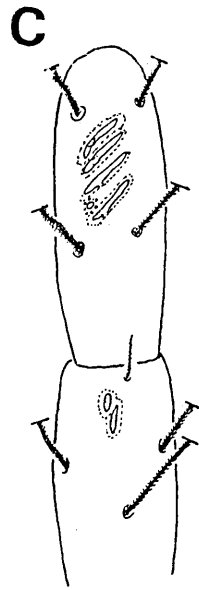
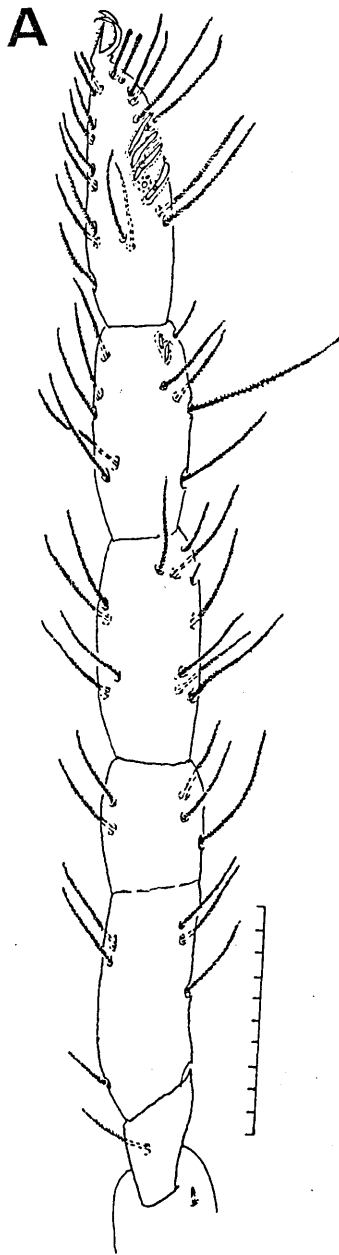


Fig. 109. *Rhagidia montana*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Rhagidia punkva Zacharda

Figs 110 & 111

Rhagidia punkva Zacharda, 1980: 575.New British record

DIAGNOSIS. *R. punkva* can be distinguished from other members of the genus by the presence of five pairs of genital setae in combination with, respectively, four and three obliquely parallel rhagidial organs on tarsi I and II, the famulus of II being absent.

Body length 631 (624-643), width 203 (195-211).

GNATHOSOMA (Figs 110C,D,E)

Subcapitulum: ratio length to width 1:0.5; internal malae short, acuminate, externals lobe-like; subcuticular setae *ca.* 39 long.

Palp: setal formula 2-3-10; tibiotalrus 2.5 times longer than wide; spiniform solenidion present.

Chelicera: total length 149 (146-153); robust, edentate chela account for one third of length; fixed digit with notch about halfway along and two terminal cusps; both setae located on fixed digit, *cha* at proximal limit, at *ca.* 13 approximately one third length of *chb*, located halfway along and overhangs end of fixed digit.

IDIOSOMA - DORSUM (Fig. 110A)

Naso: clear peak.

Setae: lengths - (*iv*) 25 (21-27), (*ev*) 23 (21-26), (*T*) 80 (77-94), (*sc*) 66 (63-69), (*c₁*) 25 (23-30), (*c₂*) 57 (50-61), (*d₁*) 29 (25-31), (*e₁*) 26 (23-28), (*f₁*) 43 (37-46), (*f₂*) 21 (18-25), (*h₁*) 63 (58-67), (*h₂*) 25 (23-29).

IDIOSOMA - VENTER (Fig. 110B)

Podosoma: setal formula 3-1-5-3; setae spatulate, 25-35 long.

Genital area: eight pairs eugenital setae, subequal, ca. 9 long; five pairs of both genital, ca. 12 long, and aggenital setae, ca. 15 long.

Anal region: (ps_1) 45(42-49), respectively a third and three times longer than (ps_2) and (ps_3) & (ad_1).

LEGS (Fig. 111)

I slightly longer than body, II and III respectively just below and above three-quarters, IV approximately body length.

Setae: formulae I 1-10(5+5)-11-11-20, II 1-10(5+5)-8-7-16, III 2-8(4+4)-6-5-13, IV 2-7(4+3)-6-6-14.

Solenidia & famuli: tarsi I and II with respectively four and three obliquely parallel rhagidial organs; famulus of tarsus I located posterolaterally between two proximal organs, that of II absent; tibiae I and II with mediodorsal spiniform solenidia; tibiae III and IV with respectively two and one proximal spines posterolaterally; genua III and IV with respectively one mediodorsal and one proximal anterolateral spine.

MALE. Sperm sac as for family.

DISTRIBUTION. Czechoslovakia, England, Wales.

MATERIAL EXAMINED. Type material: holotype ♀, CZECHOSLOVAKIA, Moravia, Moravian Kars, Skalní mlyn, wet moss near to Punkva-Creek, 4.iv.1974 (M. Zacharda) [MLU]. British material: ENGLAND, 2km SW of Walberswick, Dingle Little Hill, under gorse halfway up southern slope, from litter layer of dead grass, approximately 2cms deep, 7.i.1981.

OTHER BRITISH RECORDS. ENGLAND, Leicestershire, 12km S of Hinckley, area of oakwood edged by hawthorn, from cushion of moss by ditch at margin of wood, 19.ii.1982; Somerset, West Bagborough, 500m N of Bagborough House, area of mixed deciduous woodland, from moss on rotten branch lying on wood floor, 12.ix.1981 (K.P. Martyn); Suffolk, Dunnich Forest, area of mixed oak/beechn, from litter layer under oak tree, 9.i.1981; Yorkshire, Ilkley Moor, Cow & Calf rocks, from under stones amongst heather, 20.ii.1982. WALES, Dyfed, 1.5km N of Tregaron, Cors Tregaron, West bog, from moss (*Hypnum* sp.) amongst *Calluna* on dry ridge, 24.ii.1981; Rheidol Forest, from bracken litter by field centre, 25.ii.1981.

Fig. 110. *Rhagidia punkva*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) apex of subcapitulum, venter;
- (D) palp, antiaxial.
- (E) chelicera, antiaxial;

Scale intervals 10 μ m.

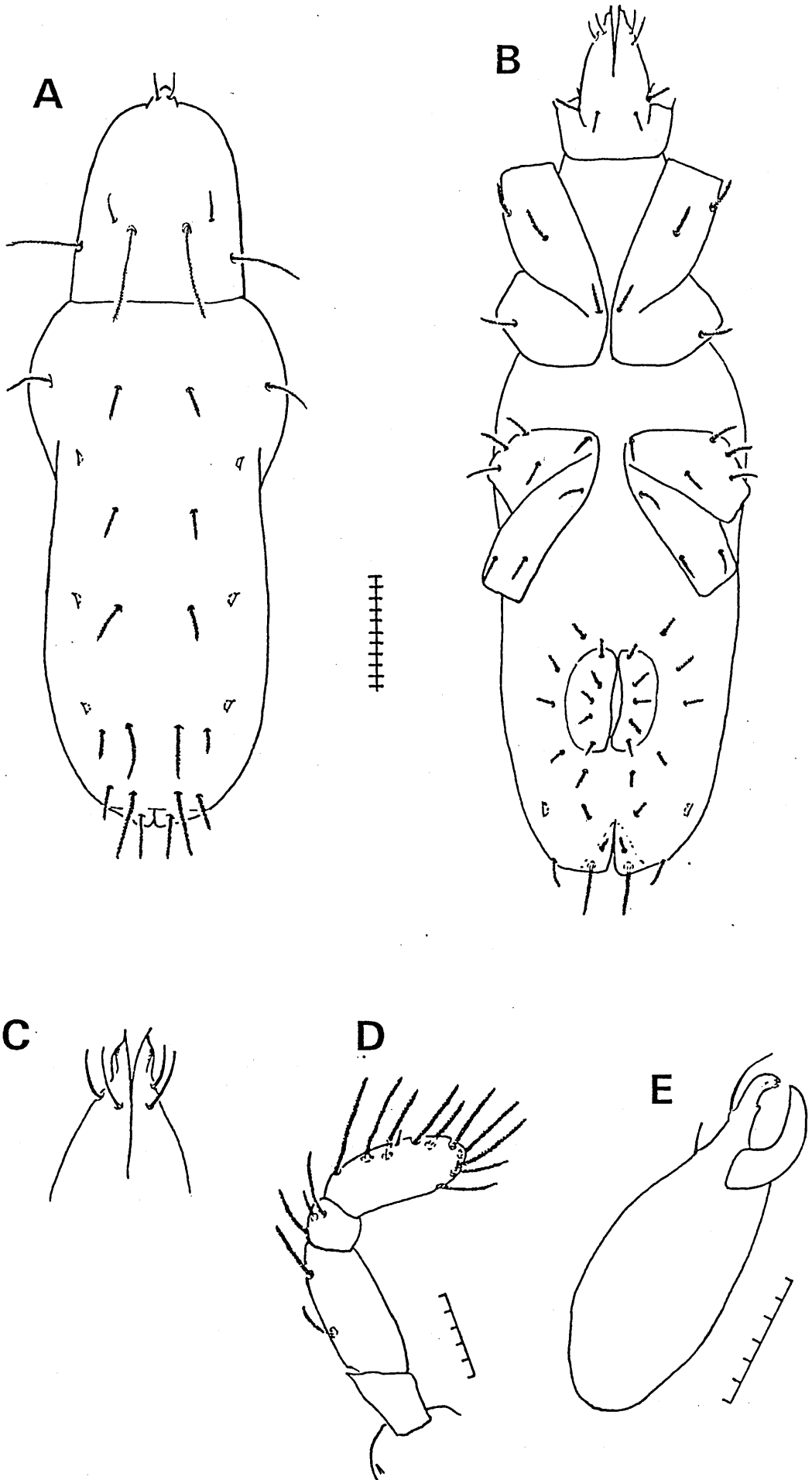
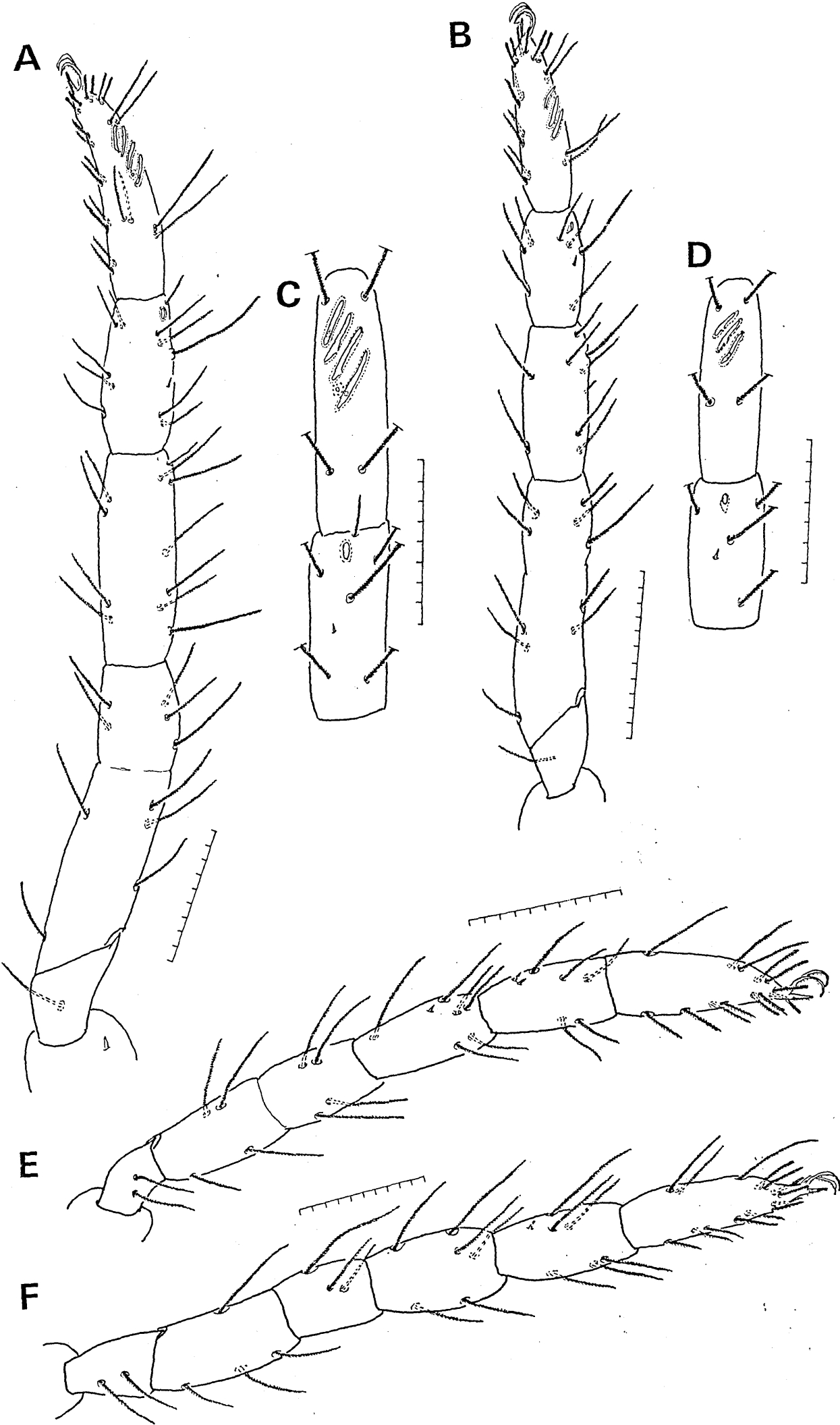


Fig. 111. *Rhagidia punkva*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Rhagidia spelaea (Wankel) comb.rev.

Figs 112 & 113

Scyphius spelaeus Wankel 1861: 258.*Rhagidia spelaea*: Thor & Willmann, 1941: 108.*Poecilophysis (Procerocheles) spelaea*: Zacharda, 1980: 617.

DIAGNOSIS. *R. spelaea* can be distinguished from other members of the genus by the combination of four rhagidial organs on tarsus I, five pairs of genital setae, six setae on coxa III and one dorsodistal rhagidial organ on tibia I.

Body length 867 (849-880), width 327 (317-338).

GNATHOSOMA (Figs 112C,D,E)

Subcapitulum: ratio length to width 1:0.6; subcapitular setae ca. 75 long.Palp: setal formula 2-3-10; spiniform solenidion present.

Chelicera: total length 256 (245-261), chela account for approximately half this; digits slender and strongly arched, fixed digit terminating in two cusps with one antiaxial tooth subterminally, movable digit finely serrate on inner margin; *cha* 19 long, *chb* 64, both located on fixed digit.

IDIOSOMA - DORSUM (Fig. 112A)

Nasq: rounded triangular with delimiting suture.

Setae: lengths - (*iv*) 48 (45-52), (*ev*) 49 (46-52), (*T*) 116 (109-122), (*sc*) 134 (128-143), (*c₁*) 59 (56-63), (*c₂*) 147 (140-155), (*d₁*) 59 (56-63), (*e₁*) 61 (57-64), (*f₁*) 102 (96-108), (*f₂*) 72 (68-77), (*h₁*) 105 (99-110), (*h₂*) 73 (68-77).

IDIOSOMA - VENTER (Fig. 112B)

Podosoma: (1a, 3a, 4a) 47 (45-50), remainder ca. twice as long.

Genital area: eight pairs eugenital setae, gradually increase in length posteriorly, from 29 to 48; five pairs genital setae, subequal, ca. 35-39 long; five pairs subequal aggenital setae ca. 55 long.

Anal region: (ps_1) 120 (115-127), (ps_2) 58 (51-63), (ps_3) and (ad_1) subequal ca. 38.

LEGS (Fig. 113)

I 1.25 times body length, II and III slightly shorter than body, IV just shorter than I.

Setae: formulae I 1-10 (5+5)-11-11-19, II 1-10 (5+5)-8-7-16, III 2-8 (4+4)-6-7-14, IV 2-7 (3+4)-6-6-13.

Solenidia & famuli: tarsus I with four obliquely parallel rhagidial organs, famulus located posterolaterally between two proximal organs; tibia I with one spinoform solenidion medially and just posterolaterally; genua I - III with a dorsodistal spine; tarsus II with three rhagidial organs in tandem in contiguous pits, though ω_2 slightly posterolateral to others; tibiae II & III with respectively one and two spines dorsoproximally; tibia IV with one proximal spine posterolaterally.

MALE. Sperm sac typical for family.

DISTRIBUTION. Belgium, Czechoslovakia, England, Federal Republic of Germany, Poland, Rumania, Wales.

MATERIAL EXAMINED. ENGLAND, Kent, by Canterbury Garden Centre, area of sparsely planted oak and *Pinus contorta*, from litter layer under pine, 17.iii.1981.

OTHER BRITISH RECORDS. ENGLAND, Kent, Westerham, Westerham Caves, from moss (*Dicranella* sp.) from damp sandy soil round cave entrance, 1.ii.1981; from damp rotten branch on floor of side passage in dark zone ca. 25m from cave entrance, 1.ii.1981; Lancashire, N. Clitheroe, Forest of Bowland, from moss mat covering ground at edge of forest, 20.ii.1982; Yorkshire, Ilkley Moor, Cow & Calf rocks, from under stones amongst *Calluna*, 20.ii.1982; Staffordshire, Cannock Chase, from bark and moss at base of silver birch, 19.ii.1982. WALES, Dyfed, 1.5km north of Tregaron, Cors Tregaron, from cracks in stone wall along margin of reserve, 24.ii.1981.

REMARKS. Wankel's description of *Scyphius spelaeus* (Wankel 1861) is inadequate for identification, while type specimens do not exist for clarification. Willmann (in Thor & Willmann 1941) redescribed this species based on topotypic material and, since his concept has gained general acceptance, I see no reason to suggest any alteration.

Fig. 112. *Rhagidia spelaea*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial.

Scale intervals 10 μ m.

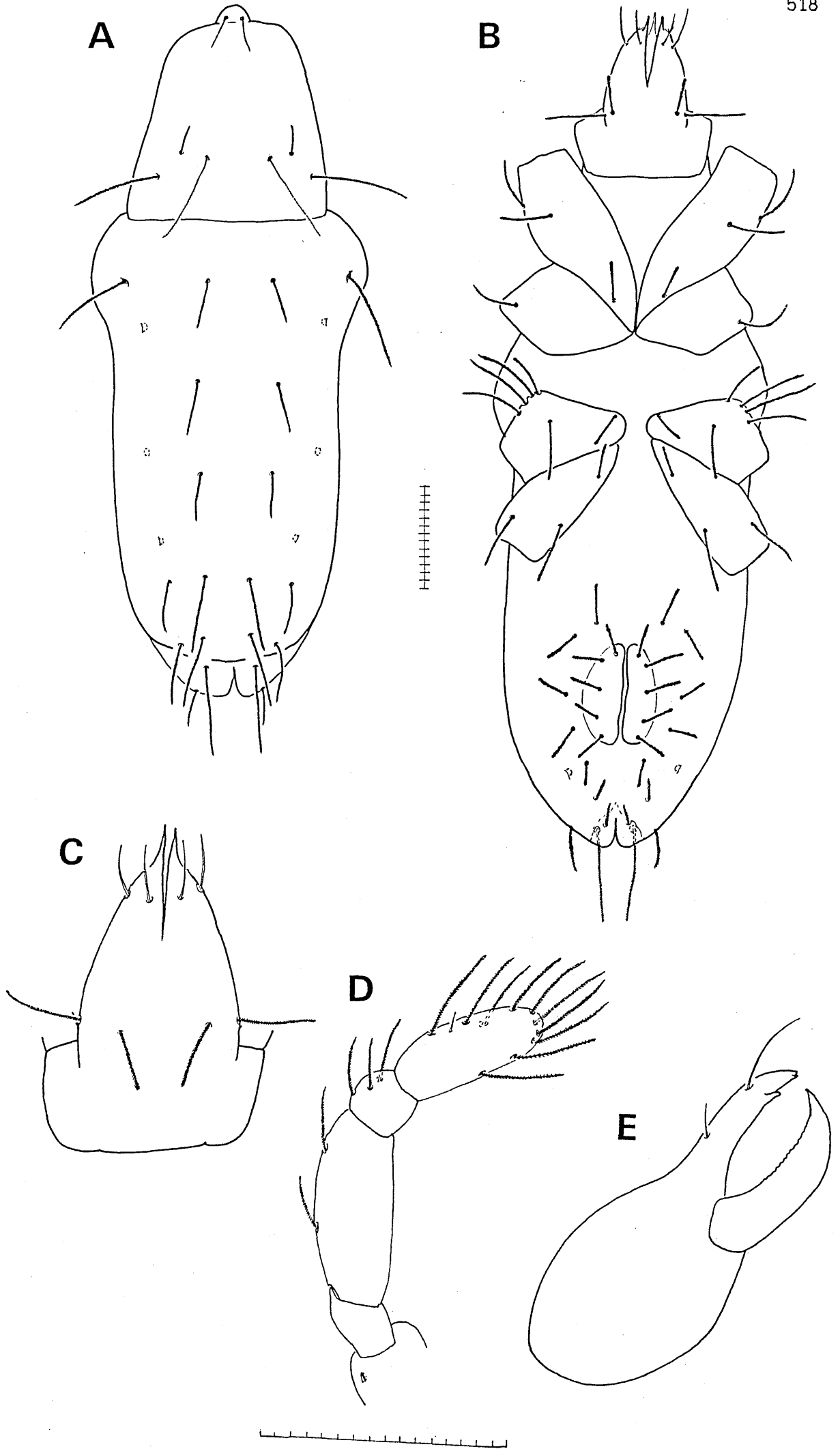
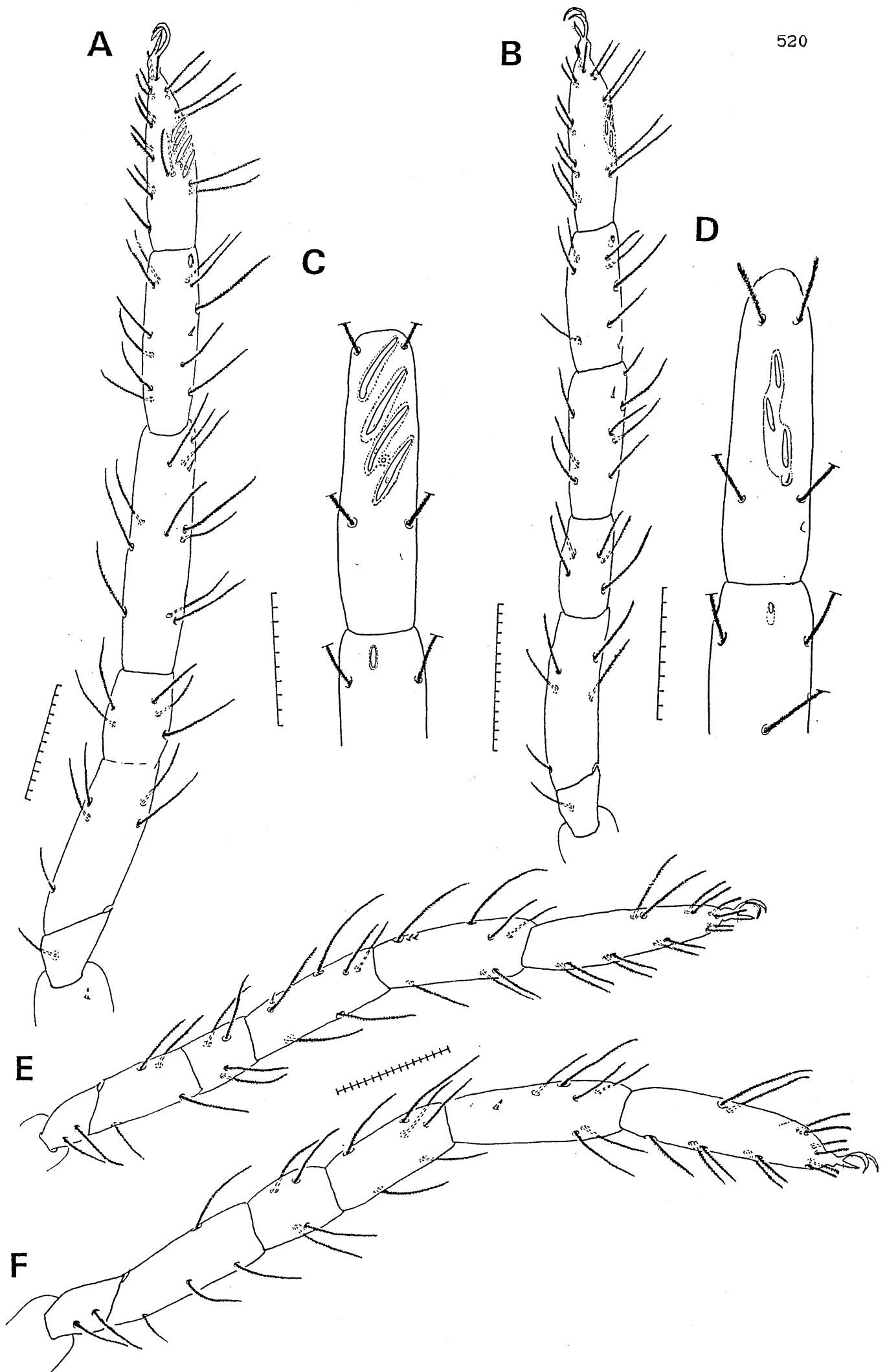


Fig. 113. *Rhagidia spelaea*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.4.2 Genus *Coccorhagidia* Thor

Coccorhagidia Thor, 1934a: 318. Thor & Willmann, 1941: 127. Strandtmann, 1971: 94.

DIAGNOSIS. *Coccorhagidia* can be distinguished from the other rhagidiid genera by the expanded trichobothria and holotrichous chaetome.

DEFINITION.

Small to large (270-1200).

Chaetome: holotrichous.

GNATHOSOMA.

Subcapitulum: internal and external malae normally differentiated, acuminate or membranous; one or two pairs adoral setae.

Palp: setal formula varies, often 2-3-10 but all segments can be deficient by one seta; length tibia-tarsus not more than twice width; solenidion present, spiniform.

Chelicera: chela account for approximately quarter to half total length, variable form; *chb* sometimes absent.

IDIOSOMA - DORSUM

Naso: a small triangular peak.

Setae: (*D*) clavate to capitate, spiculated; remainder short, extending only about quarter to third of intersetal distance, spinose.

Lyrifissures: as for family.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4,5,6-3; setae spinose.

Genital area: six to 10 pairs eugenital setae; four to five pairs densely spinose genital and aggenital setae.

Anal region: as for family.

LEGS.

All shorter than body.

Setae: generally short; densely spinose.

Solenidia & famuli: rhagidial organs T- or inverted U-shaped; I with four, rarely three, rhagidial organs arranged obliquely parallel; tarsus II with two, three or four rhagidial organs, variously arranged; one rhagidial organ distally on tibia I and II; erect spiniform solenidia on most tibiae and genua, occasionally also on tarsi and femora.

Apotela: all or similar form; rarely, with small empodial claw.

MALE. Sperm sac as for family.

TYPE SPECIES. *Noerneria clavifrons* Canestrini.

DISTRIBUTION. Cosmopolitan.

REMARKS. Three species of *Coccorhagidia* have previously been recorded from the British Isles: *C. subterranea* (Evans 1952); *C. berlesei* (Wood 1967); *C. clavifrons* (Luxton 1966, Wood 1967). *C. berlesei* is here synonymized with *C. subterranea* (see below), while *C. clavifrons* was also collected in the present study.

Key to the British species of *Coccorhagidia*

1. famuli enlarged, elaborately branched; distal rhagidial organ of tarsus I inverted U-shaped *C. macrostella*
- famuli normal; distal rhagidial organ of tarsus I T-shaped 2
2. four rhagidial organs on tarsus II 3
- two or three rhagidial organs on tarsus II 4
3. body length around 500; palp genu with two setae; coxa III with six setae; four pairs aggenital setae *C. clavifrons*
- body length around 600; coxa III with five setae; palp genu with three setae; five pairs aggenital setae *C. pittardi*
4. palp genu with one seta; three rhagidial organs on tarsus I & II *C. subterranea*
- palp genu with two setae; respectively four and two rhagidial organs on tarsus I and II *C. evansi*

Coccorhagidia clavifrons (Canestrini)

Figs 114 & 115

Noerneria clavifrons Canestrini, 1836: 710*Coccorhagidia clavifrons*: Thor & Willmann, 1941: 128; Meyer & Ryke, 1960: 493; Strandtmann & Prasse, 1976: 13; Strandtmann & Goff, 1978: 143; Zacharda, 1980: 704; Zacharda, 1983: 316.

DIAGNOSIS. The type species of the genus, *C. clavifrons* can be distinguished from other members by the presence of four obliquely parallel rhagidial organs on tarsi I and II and by the palp setal formula of 2-2-10.

Body length 491 (478-513), width 172 (163-181).

GNATHOSOMA (Figs 114C,D,E)Subcapitulum: subcapitular setae 13-15 long; two pairs adoral setae.Palp: setal formula 2-2-10; ω present.Chelicera: total length ca. 139 (133-145); chela account for approximately one third total length; fixed digit robust, tapers to point; movable digit sickle-shaped, robust in proximal quarter then narrows suddenly; two setae, inserted on small tubercle, *cha* located at base of fixed digit, at ca. 10 just below half length of *chb*.**IDIOSOMA - DORSUM** (Fig. 114A)Naso: as for genus.Setae: (*T*) clavate; lengths - (*ev*) ca. 8, (*T*) 55 (53-58), (*sc*) 50 (47-53), (*ca*) 28 (25-31), (*h*) 24 (22-27), remainder ca. 10.**IDIOSOMA - VENTER** (Fig. 114B)Podosoma: formula 3-1-6-3; setae subequal ca. 16 long.

Genital area: six pairs eugenital setae ca. 7 long; five pairs genital setae ca. 9 long; four pairs aggenital setae ca. 12 long.

Anal region: (ps₁) ca. 24, remaining setae subequal, ca. 9.

LEGS (Fig. 115)

I approximately three-quarters body length, II and III half body length, IV just shorter than I.

Setae: formulae I 1-11(6+5)-11-10-18, II 1-11(6+5)-8-7-14,

III 2-8(4+4)-6-5-12, IV 2-6(3+3)-6-6-12.

Solenidia & famuli: tarsi I and II both with four dorsal, obliquely parallel organs, famuli of I and II respectively between posterolateral limits of middle and distal two organs; tibia I with long dorsodistal spine just posterior to small rhagidial organ, tibia II as for I but spine shorter; spine distally and anterolaterally on genu I, dorsomedially on genu II, proximally and just posterolaterally on genu III; two spines dorsoproximally on tibia III, one proximally and just anterolaterally on tibia IV.

MALE. Sperm sac as for family.

DISTRIBUTION. Czechoslovakia, German Democratic Republic, Eire, England, Hawaii, Italy, Japan, Republic of South Africa, Scotland, USSR.

MATERIAL EXAMINED. British material: ENGLAND, Suffolk, Dingle Great Hill, 2km SW of Walberswick, with cover of gorse and grass surrounding areas of *Erica cinerea*, from *Agrostis*, *Cladonia*, *Pleurozium schreberi* plus underlying 2cm of soil, 7.i.1981; Westleton Heath, 1500m NE of Westleton, undulating heathland surrounded by gorse, from bracken litter plus *Polytrichum* moss at edge of heath, 9.i.1981.

OTHER BRITISH RECORDS. EIRE, Galway, 22 miles NE of Galway, Ryehill, Monivea, beech copse, from litter covered with moss inside hollow of beech tree, 20.viii.1981 (K. P. Martyn). ENGLAND, Essex, Colne Point, Nature Reserve, approximately 500m south of North Mud Flats and 30m inland from North Horse Wash inlet along *Sueda* path, from aerial parts of sea purslane and approximately 3cm of dark, damp soil, 12.v.1981; Yorkshire, Boltons Abbey, from moss on stone wall by village hall, 20.ii.1981. SCOTLAND, Highland, Ben Eighe, by Stop 6 of mountain path, from well rotted pine tree-hole litter, 16.ix.1982. WALES, Dyfed, Rheidol Forest, approximately 20m from edge of forest, from hemlock litter and fermentation layer, 26.ii.1981.

Fig. 114. *Coccorhagidia clavifrons*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) palp, antiaxial;

(D) chelicera, antiaxial.

Scale intervals 10 μ m.

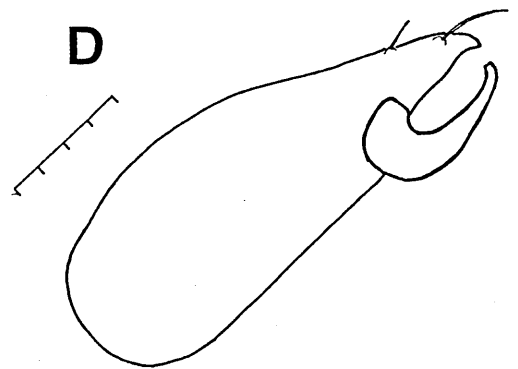
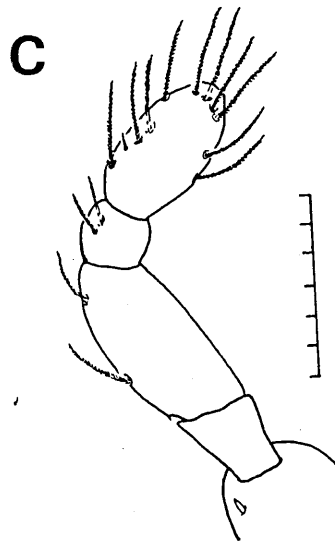
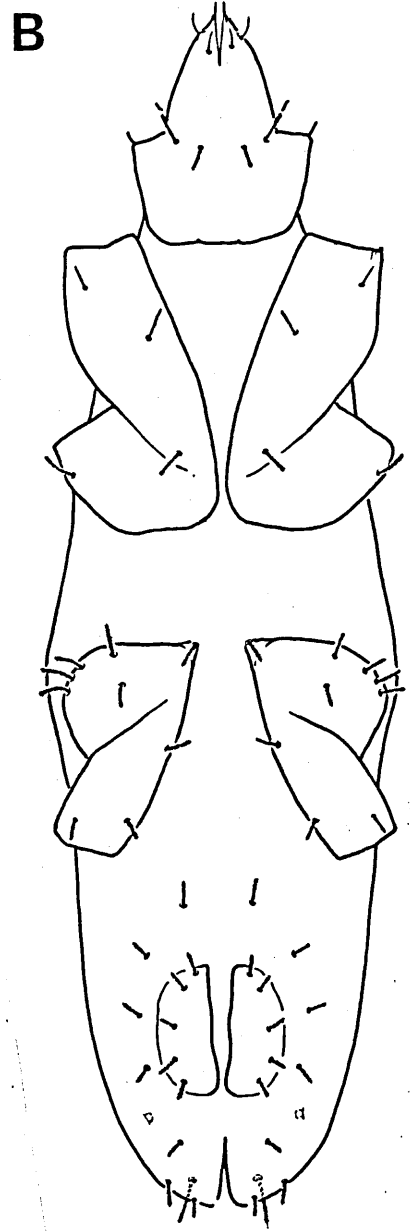
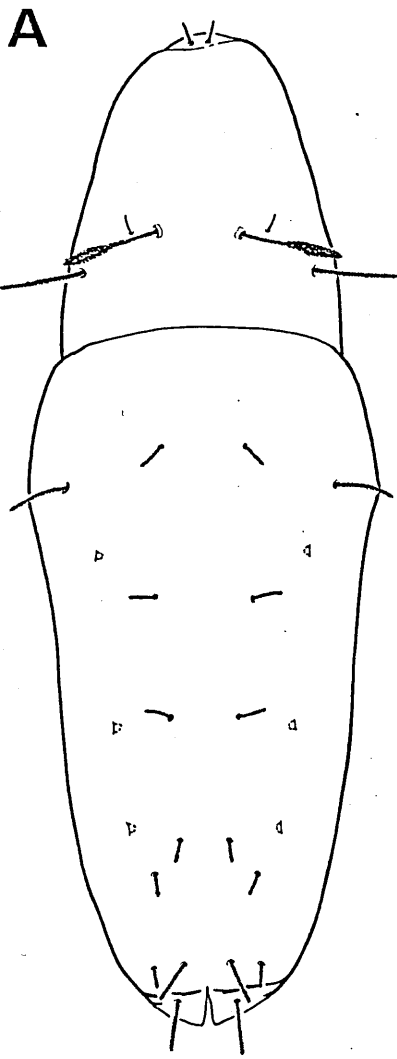
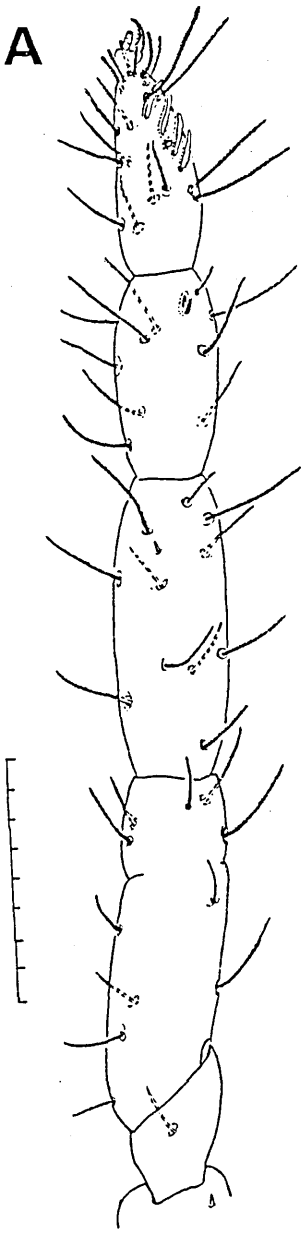


Fig. 115. *Coccorhagidia clavifrons*:

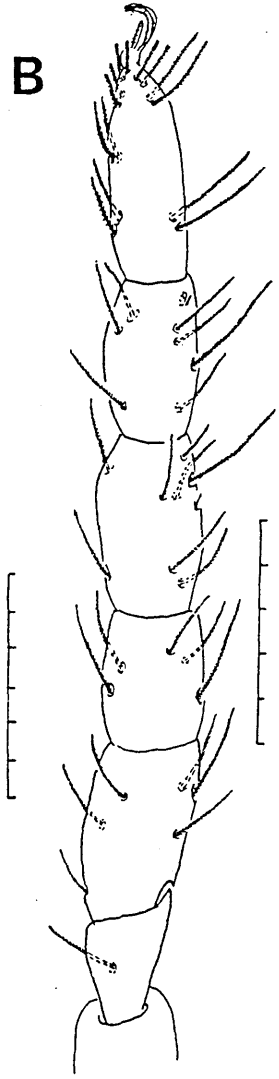
- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.

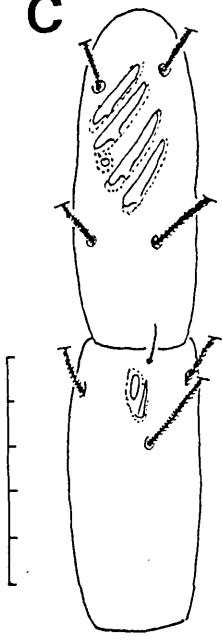
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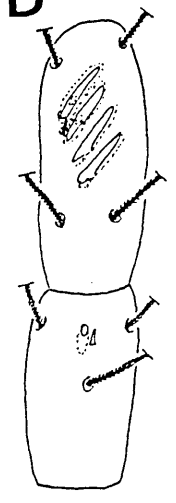
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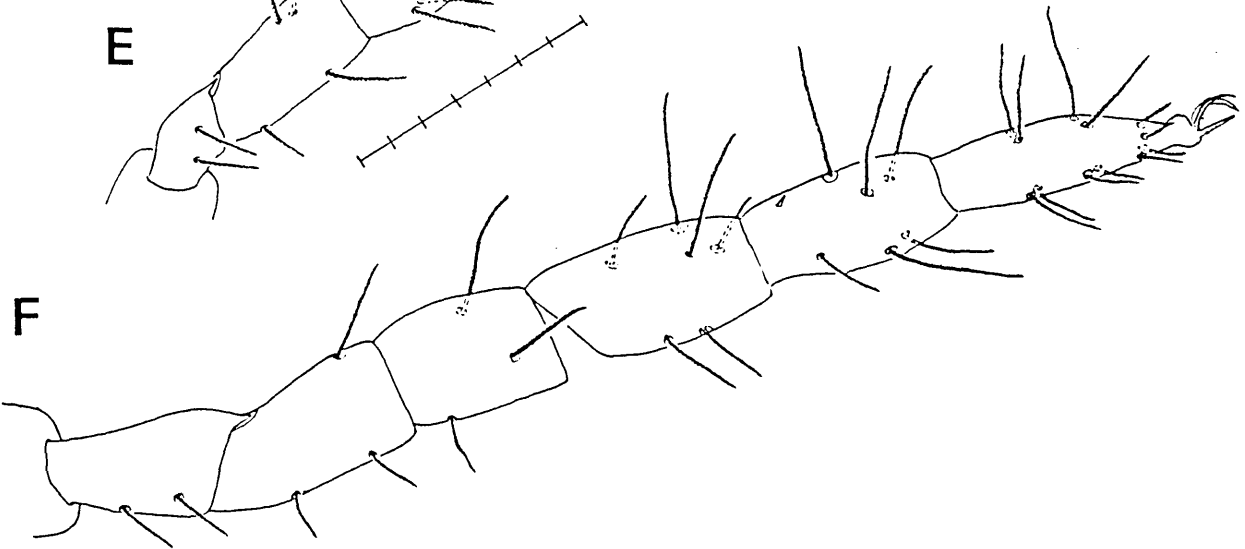
D



E



F



Coccorhagidia evansi comb. rev.

Figs 116 & 117

Coccorhagidia evansi Strandtmann & Prasse 1976: 12.

Parallelorhagidia evansi: Zacharda, 1980: 591.

New British record

DIAGNOSIS. *C. evansi* can be distinguished from other members of the genus by the presence of, respectively, two and nine setae on the palp genu and tibiotarsus and four and two rhagidial organs on tarsus I and II.

Body length 314 (275-341); width 112 (102-127).

GNATHOSOMA (Figs 116C,D,E)

Subcapitulum: ratio length to width 1:0.6; internal malae short, pointed; external malae broad, membranous; subcapitular setae subequal, ca. 10 long; two pairs adoral setae.

Palp: setal formula 2-2-9; ω present; tibiotarsus robust, length 1.8 times width.

Chelicera: total length 68 (65-71), chela accounting for approximately one third of this; *cha* 6 long, located slightly antiaxially and proximal to fixed digit; *chb*, 15 long, inserted dorsally at base of fixed digit; inner margin of both digits smooth; fixed digit narrows suddenly in distal third.

IDIOSOMA - DORSUM (Fig. 116A)

Naso: inconspicuous, a slight extension of prodorsum.

Setae: (*T*) clavate, remainder spinose; lengths (*iv*) 9, (*ev*) 17, (*sc*) 24, (*T*) 30, (*c*₁) 12, (*c*₂) 16, (*d*₁) 11, (*e*₁) 11, (*f*₁) 12, (*f*₂) 9, (*h*₁) 21, (*h*₂) 12.

IDIOSOMA - VENTER (Fig. 116B)

Podosoma: proximal limits of epimeres faintly defined; setal formula 3-1-4-3; subequal, ca. 11-13 long.

Genital area: 12 pairs eugenital setae, subequal, ca. 7 long, five pairs of both genital and aggenital setae, subequal, ca. 11 long; three gravid females all with a single large, round egg, ca. 90 long.

Anal region: (*ad*₁) and (*ps*₃) subequal ca. 7 long, (*ps*₁ & *2*) respectively 19 and 13 long.

LEGS (Fig. 117)

Robust; I and IV approximately two-thirds body length, II and III just over half body length.

Setae: formulae I 1-10(5+5)-11-11-16, II 1-10(5+5)-7-7-14, III 2-8(4+4)-6-4-12, IV 2-8(4+4)-6-6-12; all short, shorter than segments.

Solenidia & famuli: tarsus I with four, subequal, T-shaped rhagidial organs in distal half of segment, arranged level and parallel to longitudinal axis of leg, famulus located between two posterolateral organs; tarsus II with two T-shaped rhagidial organs lying parallel and obliquely in median third of segment, famulus located at base of posterolateral organ; tibia I and II with distal slightly posterolateral rhagidial organ and dorso-proximal spine; tibia III with two adjacent

proximal anterolateral spines; genua I-III with one spine, that of I located ventro-distally, of II and III ventro-proximally.

MALE. Unknown.

DISTRIBUTION. Czechoslovakia, England, German Democratic Republic, Scotland.

MATERIAL EXAMINED. Type material: Holotype ♀, GERMAN DEMOCRATIC REPUBLIC, Etdorf/Saalkreis Experimental Farm, Slide 79 [MLU]. Collection details given as under winter wheat and oats up to a depth of 20cm, during summer months. British material: ENGLAND, Suffolk, Westleton Heath, approximately 1 mile NE of Westleton, undulating heathland surrounded by gorse, from litter layer of bracken plus *Polytrichum* moss at edge of heath, 9.i.1981; Cambridgeshire, Woodwalton fen, by dyke and main path along eastern side, south of junction between compartments 80 & 84, from rotten purple willow (*Salix purpurea* litter, 30.vi.1981.

OTHER BRITISH RECORDS. ENGLAND, Kent, 4.5km NE of Canterbury, Westbere Marshes, on west shore of lake, from moss between *Phragmites*, 16.iii.1981. SCOTLAND, Strathclyde, western shore of Loch Lomond, from bracken litter in birch copse, 12.ix.1982; Sutherland, Torboll, near Golspie, from alder carr grass and leaf litter, 29.vi.1976 (P.D. Hillyard).

REMARKS. Strandtmann and Prasse (1976) figure the famulus of tarsus I between the two median rhagidial organs but state that it occurs 'between

the outer two'. It is here confirmed (in agreement with Zacharda (1980)) that the latter situation is true.

In the original description of this species, the idiosomal length is given the wide range of 250-420 μ , and Strandtmann and Prasse note certain variations in form between a 'smaller' and a 'larger' form. Unfortunately, apart from palp chaetotaxy, these variations are not explained but it is possible that more than one species was present in the sample examined. The idiosomal length of the holotype is 300 μ , however, and so it is a 'smaller form'.

Having examined Berlese's specimens of *Rhagidia subterranea* and those described by Evans (1952), Strandtmann and Prasse's opinion that these are not conspecific with *C. evansi* is here supported.

Fig. 116. *Coccorhagidia evansi*:

(A) idiosoma, dorsum;

(B) idiosoma, venter;

(C) palp, antiaxial;

(D) chelicera, antiaxial.

Scale intervals 10 μ m.

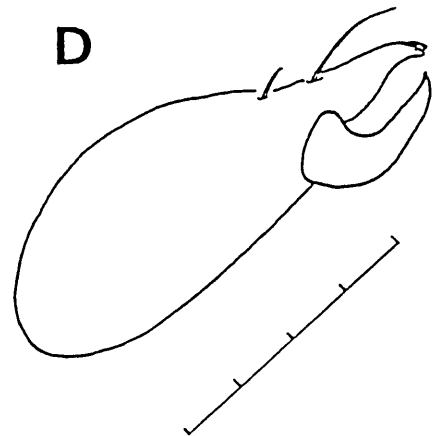
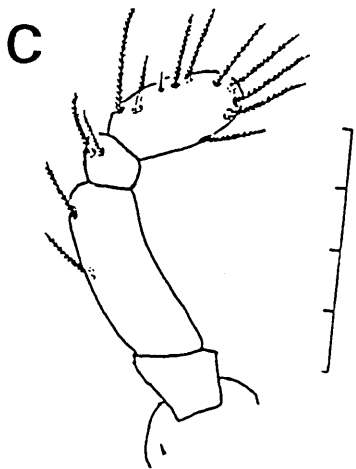
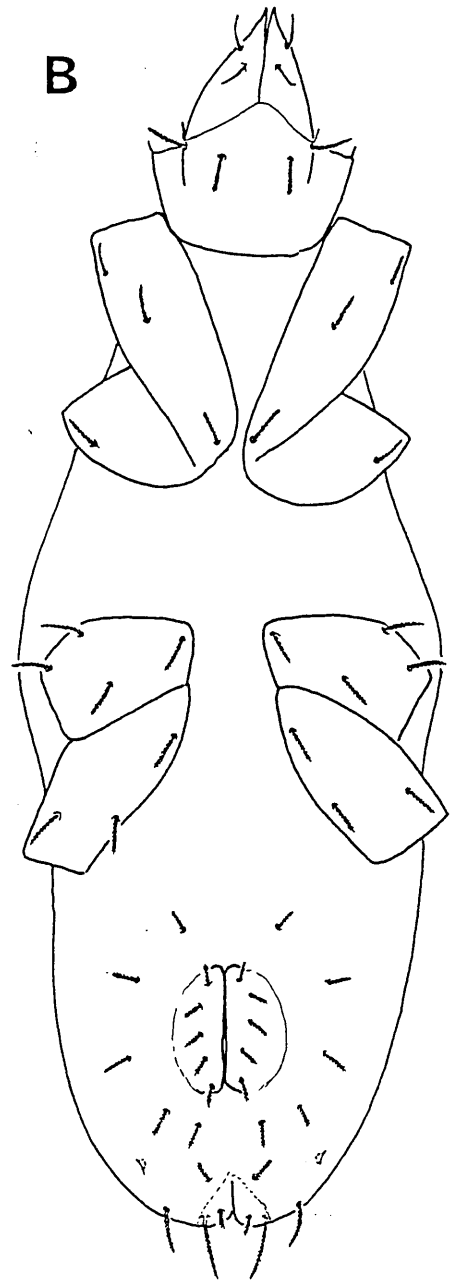
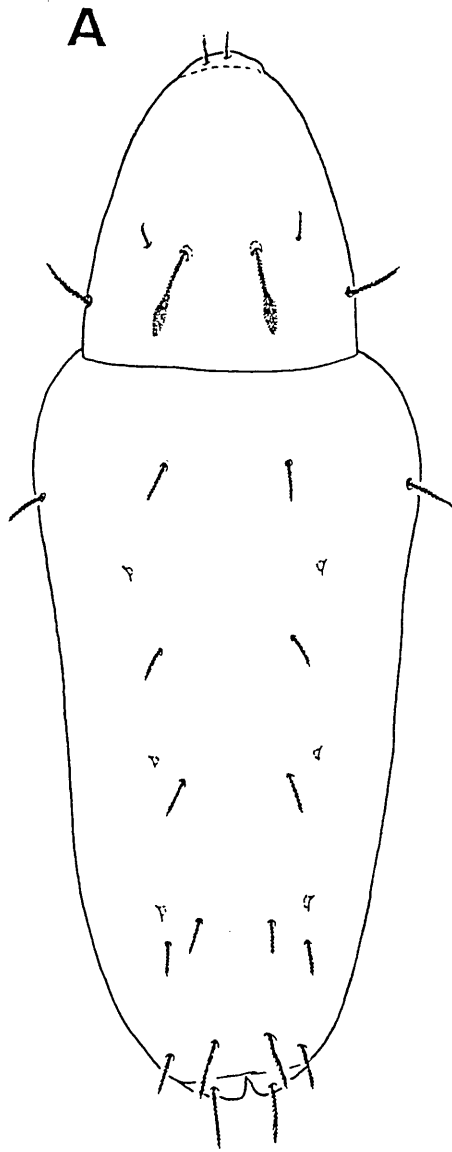
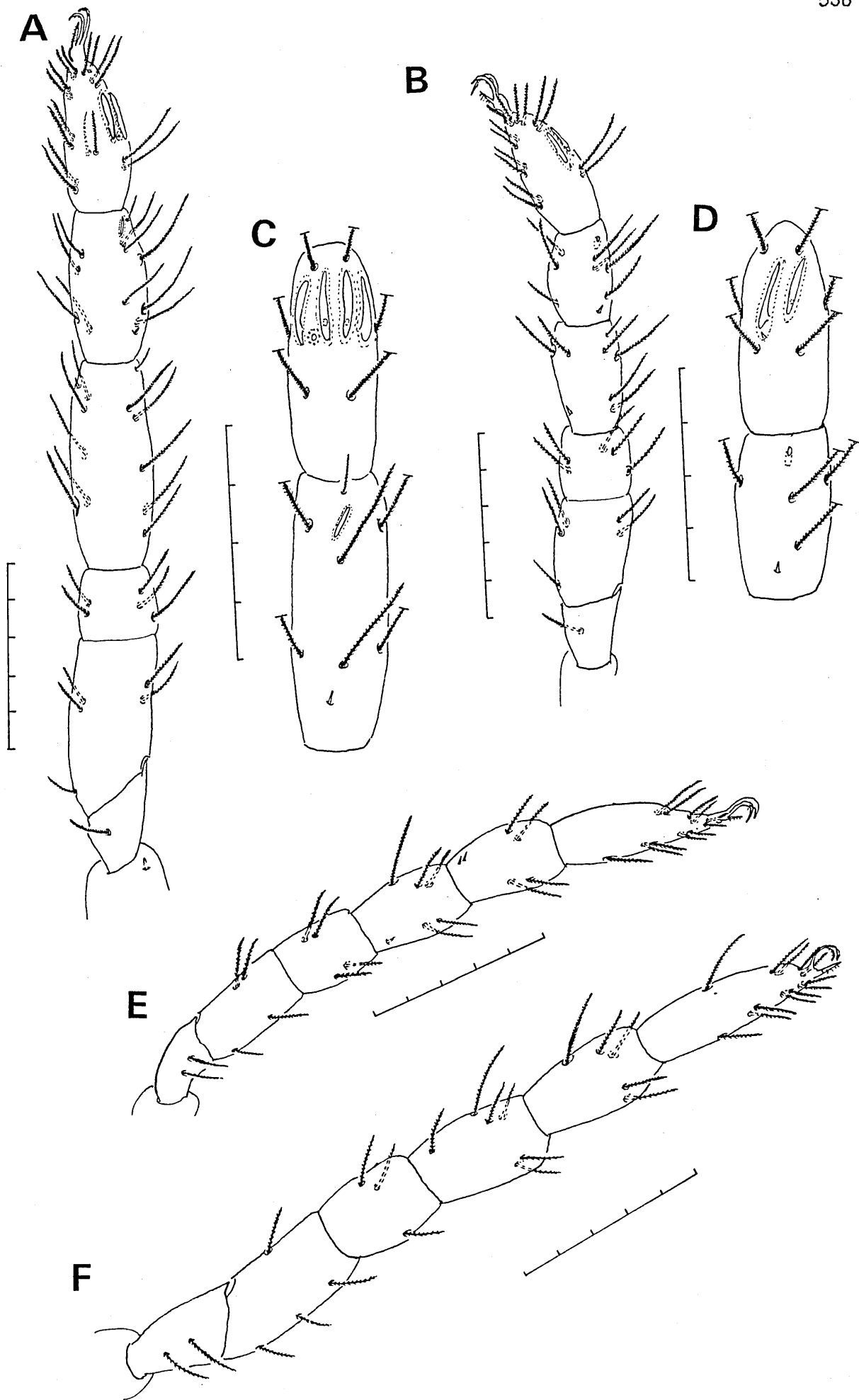


Fig. 117. *Coccorhagidia evansi*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Coccorhagidia macrostella Zacharda n.comb.

Figs 15c, 17e, 18d, 19g, 20a, 25b, 27b, 118 & 119

Hammenia macrostella Zacharda, 1980: 760.New British record

DIAGNOSIS. *C. macrostella* can immediately be distinguished from the other members of the genus by the inverted U-shaped rhagidial organ on tarsus I and the enlarged and elaborately branched famuli.

Body length 272 (250-308), width 127 (117-136).

GNATHOSOMA (Figs 118C,D,E)

Subcapitulum: subcapitular setae 8-10 long; one pair adoral setae.

Palp: setal formula 2-3-9; setae heteromorphous; spiniform solenidion present.

Chelicera: total length 58 (55-63); robust, strongly chelate; chela account for almost half total length; *cha* inserted dorsally at base of fixed digit, on small tubercle, *ca.* long; *chb* absent; fixed digit deflected dorsally, terminates in 3 cusps, fairly slender but with anterolateral membranous portion; movable digit much expanded, 'veined', with median and terminal tooth, serrated along rest of length.

IDIOSOMA - DORSUM (Figs 15c, 20a, 118A)

Naso: as for genus, in lateral view appears erect.

Setae: (*T*) clavate, stalk approximately twice length of expanded part, inserted in markedly deep bothridia; lengths - (*iv*) 5-8, (*ev*) 7-9, (*T*) 34-40, (*sc*) 14-16, (*c₁*) 12-14, (*c₂*) 14-16, remainder subequal *ca.* 12.

IDIOSOMA - VENTER (Figs 25b, 118B)

Podosoma: formula 3-1-4-3; setae subequal, ca. 16 long.

Genital area: five pairs spinose tapering eugenital setae, ca. 5 long; four pairs spinose genital and aggenital setae, subequal at 7 long.

Anal region: setae plumose; (ps_1) 11-13 long, (ps_2 & 3) subequal ca. 8-10, twice length of (ad_1).

LEGS (Figs 17e, 18d, 19g, 27b, 119)

I approximately two-thirds body length, II and III about half, IV slightly shorter than I.

Setae: formulae I 1-10(5+5)-6-9-18, II 1-10(5+5)-6-5-14,

III 2-8(4+4)-6-4-12, IV 2-7(4+3)-6-4-10.

Solenidia: tarsus I with four rhagidial organs, distal an inverted U-shape encompassing large famulus with elaborately branched processes; tibia I with one slightly posterolateral distal rhagidial organ and one proximal spine; tarsus II with four staggered parallel rhagidial organs in separate pits, elaborately branched famulus just posterolateral to proximal organ; tibia II same configuration as I; anterolateral ventral spine medially on genu II, tibia III and genu IV, proximally on genu III and distally on femur IV.

Apotela: empodia with small terminal claw.

DISTRIBUTION. Czechoslovakia, England, Scotland, Wales.

MATERIAL EXAMINED. Type material: Holotype ♀, CZECHOSLOVAKIA, Bohemia bor., Velky Bezedz-Hill, rocky steppe on southern slope, grass rhizosphere, 11.iii.1973 (M. Zacharda) [MZ]. British material: ENGLAND, Suffolk, 2km SW of Walberswick, Dingle Great Hill, from *Erica cinerea* covered soil amongst gorse, 9.i.1981; Kent, Westbere Marshes, for moss and grass, 16.iii.1981.

amongst gorse, 9.i.1981; Kent, Westbere Marshes, for moss and grass, 16.iii.1981.

OTHER BRITISH RECORDS. ENGLAND, Wiltshire, Savernake Forest, birch copse in east part of forest, from moss round base of birch tree, 17.ix.1981; Devon, Braunton Burrows, moss overlying sand on slacks, 7.xii.1981.

SCOTLAND, Grampian, Cairngorm Mountains, 100m above middle station, from *Lycopodium* sp. moss, 17.ix.1982; Sutherland, SW of Torball, from heather litter, 29.vi.1976 (P. N. Lawrence). WALES, Dyfed, 2km N of Tregaron, Cors Tregaron, raised *Sphagnum* bog, from *Hypnum* sp. moss on dry ridge with *Calluna*, 24.ii.1981; Borth, Ynyslas Nature Reserve, mature sand dunes approximately 200m from beach, from mat of mixed mosses growing amongst marram grass, 24.ii.1981.

REMARKS. Examination of the holotype of *Hammenia macrostella* revealed the presence of the U-shaped rhagidial organ on tarsus I. Although Zacharda (1980) figures a pit of this shape surrounding the famulus, he did not describe the solenidion lying in it. Also, an elaborately branched famulus on tarsus II was observed whereas Zacharda reports it as absent. The trochanteral setal formula of 1-1-2-2 was confirmed for this species. Zacharda remarks on the variability of genital and aggenital setae. In this study, however, the complement was consistently found to be four pairs in both cases.

H. macrostella is a widespread species most frequently found in mossy habitats.

Fig. 118. *Coccorhagidia macrostella*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial.

Scale intervals 10 μ m.

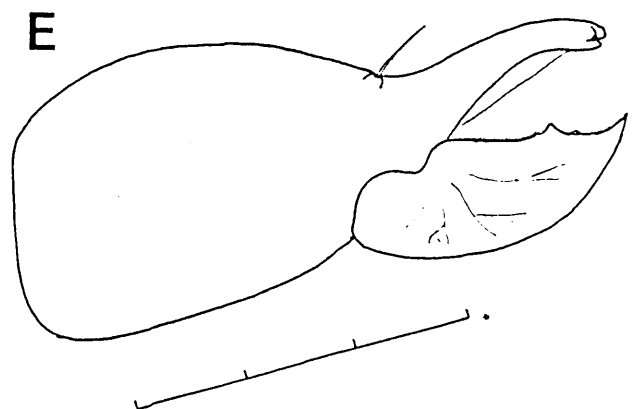
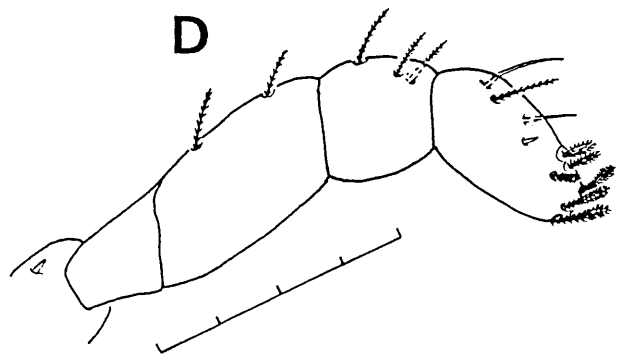
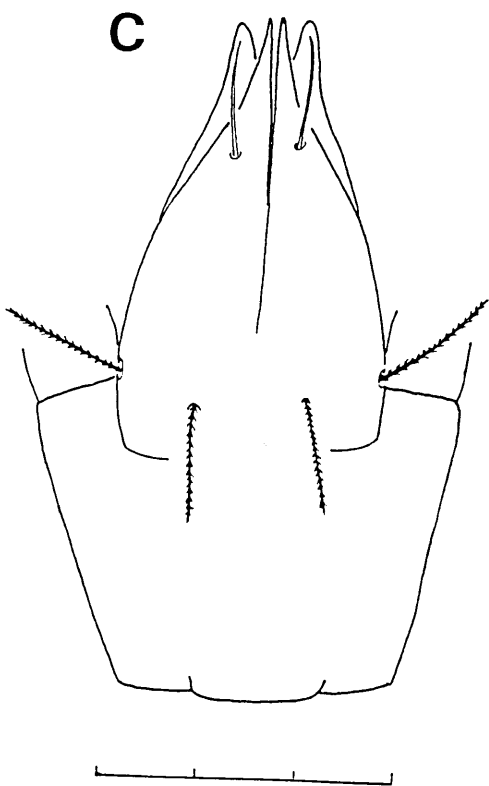
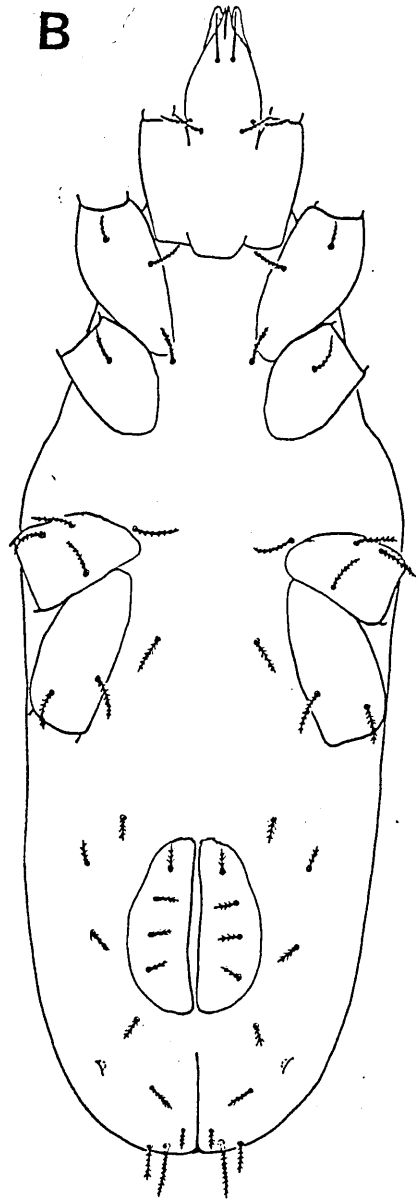
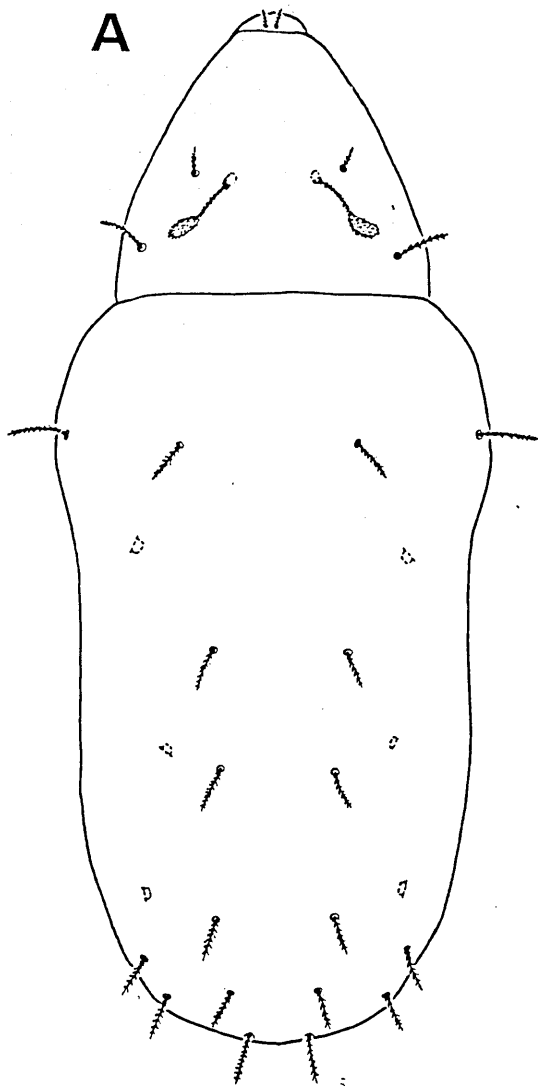
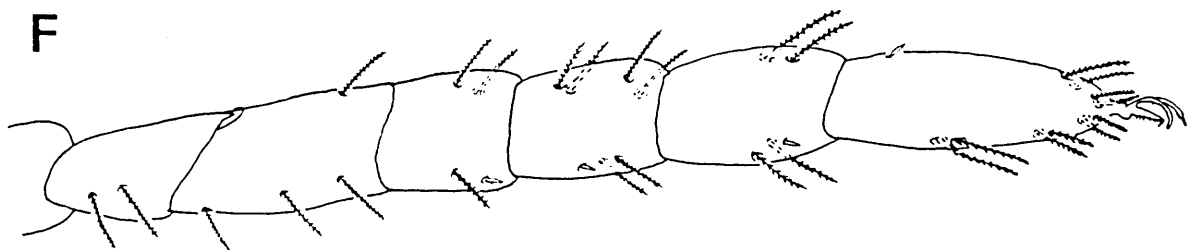
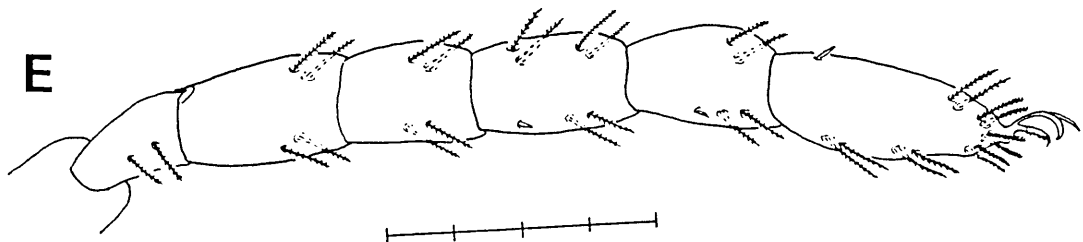
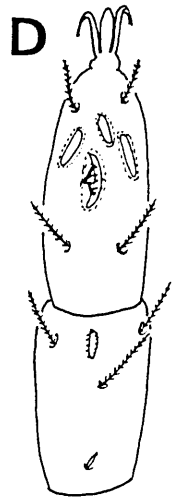
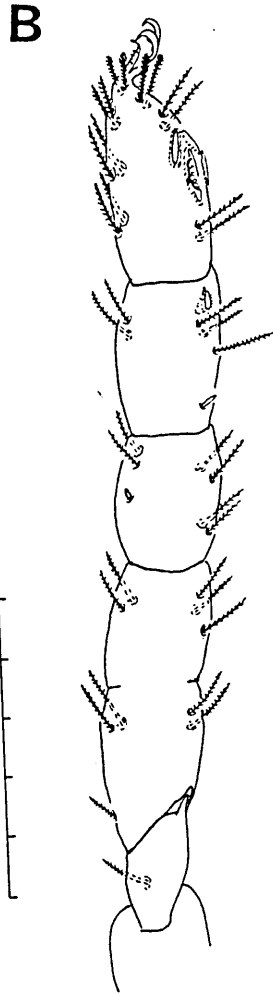
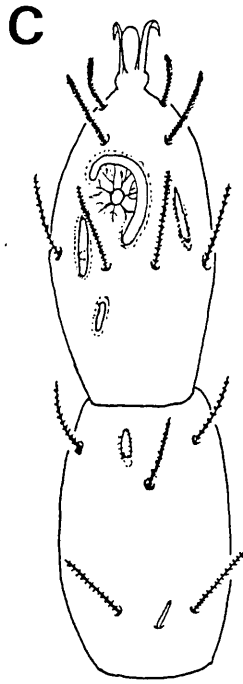
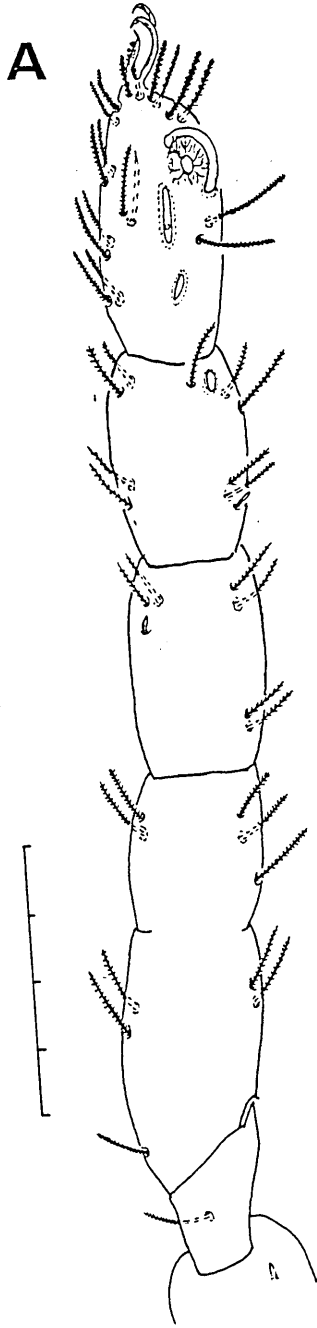


Fig. 119. *Coccorhagidia macrostella*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



Coccorhagidia pittardi Strandtmann

Figs 120 & 121

Coccorhagidia pittardi Strandtmann, 1971: 98. Zacharda, 1980: 708.

DIAGNOSIS. *C. pittardi* can be distinguished from other species of the genus by the presence of four rhagidial organs on tarsi I and II and the location of the famulus of tarsus II between the two proximal organs in combination with five setae on coxa IV and, respectively, 10 and five pairs of eugenital and genital setae.

Body length 632 (617-649), width 205 (198-211).

GNATHOSOMA (Figs 120B,C,D)

Subcapitulum: ratio length to width 1:0.8; internal malae needle-like, external malae membranous lobes; subcapitular setae blunt ca. 28 long; two pairs adoral setae.

Palp: setal formula 1-3-10.

Chelicera: total length 127 (119-138); robust chela account for just under one third of length; movable digit sickle-shaped; fixed digit stout, hardly curved; *cha* and *chb* both located dorsally on fixed digit; *cha*, at 12 long, approximately one third *chb*.

IDIOSOMA - DORSUM (Fig. 120A)

Naso: as for genus.

Setae: (T) clavate, swollen head half as long as stalk, spiculed; remainder spinose, mostly short, ca. 16 long, although (*sc*), (*h₁*) and (*c₂*) noticeably longer, ca. 30-35.

IDIOSOMA - VENTER (Fig. 120B)

Podosoma: setae spinose, subequal, ca. 30 long; formula 3-1-5-3.

Genital area: 10 pairs eugenital setae, ca. 12 long; five pairs both genital and aggenital setae, respectively ca. 12 and 16 long.

Anal region: (ps₁) at ca. 35 approximately three times longer than other setae.

LEGS (Fig. 121)

I and IV just below body length, II and III respectively just above and below three-quarters body length.

Setae: formulae I 1-10(5+5)-11-11-17, II 1-10(5+5)-8-7-14,

III 2-8(4+4)-6-6-12, IV 2-7(4+3)-6-6-11.

Solenidia & famuli: tarsi I and II both with four obliquely parallel rhagidial organs, but in separate pits; I with famulus posterolaterally between two median organs; II with famulus posterolaterally between two proximal rhagidial organs; tibiae I and II both with small distal rhagidial organ and proximal spine slightly posterolaterally; tibia III with two spines just posterolaterally on proximal part of segment, tibia IV with just one spine in this position; genu III with one proximal posterolateral spine.

MALE. Unknown.

DISTRIBUTION. Czechoslovakia, England, Alaska, Scotland, Wales.

MATERIAL EXAMINED. Type material: holotype ♀, ALASKA, Anaktuvik Pass, 17.vi.1968 (Kay & Don Pittard) [BM, slide no. 9347]. **British material:** ENGLAND, Cornwall, 4km NW of Saltash, from grass in crevice of roadside granite wall, 19.xii.1981; Surrey, Chobham Common, from *Polytrichum* moss amongst *Calluna*, 19.v.1982.

OTHER BRITISH RECORDS. ENGLAND, Yorkshire, Ilkley Moor, by Cow and Calf rock, from moss and *Calluna* roots, plus adhering soil, growing over stones, 20.ii.1981. SCOTLAND, Grampian, Craigellachie, area of birch woodland, from rotten birch branch on floor of wood, 17.ix.1982; Highland, Cairngorms, by middle station of chair lift, from dry *Sphagnum* covering hummock amongst rocks, 17.ix.1982. WALES, Dyfed, Borth, Ynyslas Nature Reserve, slacks between mature dunes approximately 200m from top of beach, mixed mosses plus 1cm of underlying sandy soil, 25.ii.1981.

Fig. 120. *Coccorhagidia pittardi*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) palp, antiaxial;
- (D) chelicera, antiaxial.

Scale intervals 10 μ m.

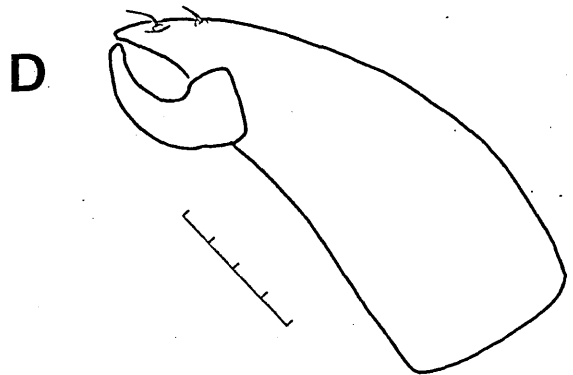
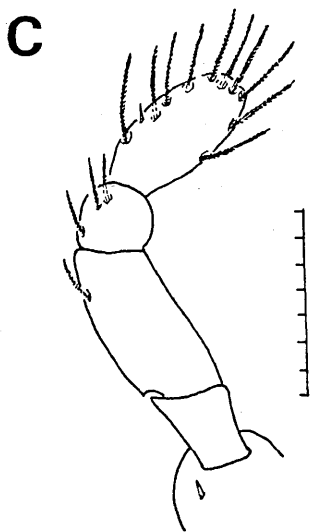
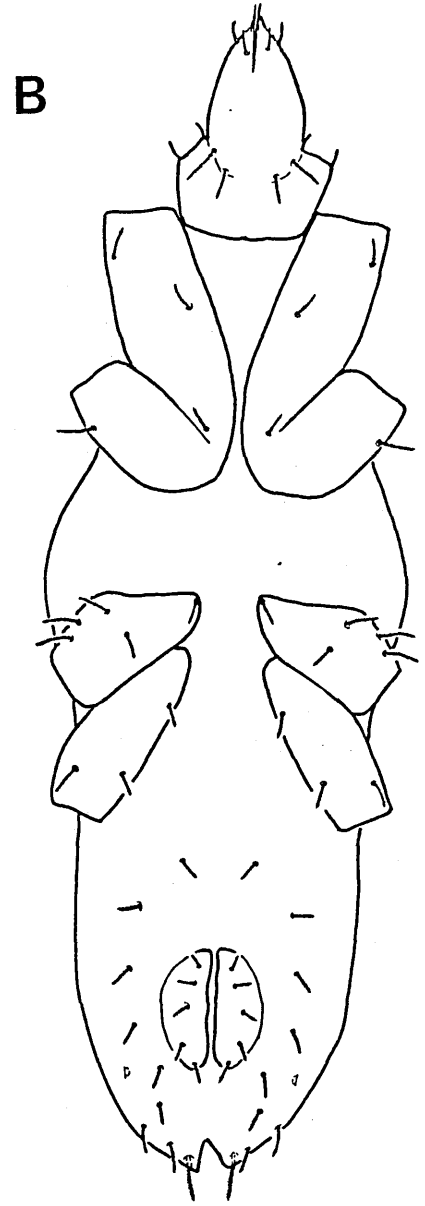
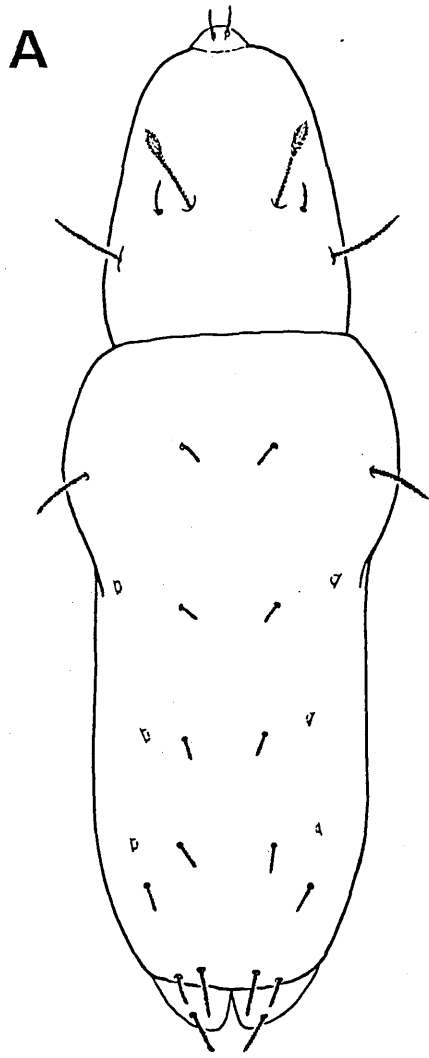
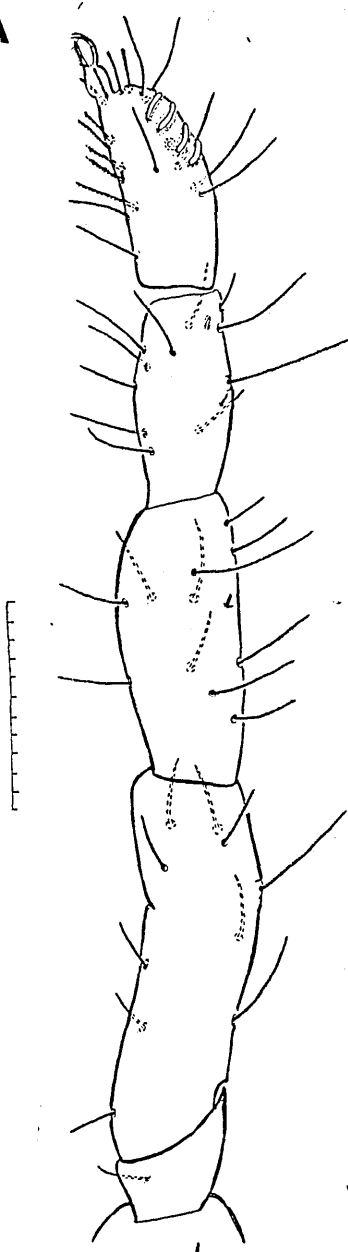


Fig. 121. *Coccorhagidia pittardi*:

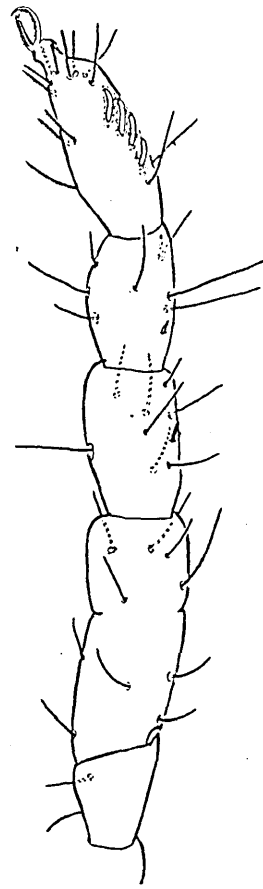
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- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.

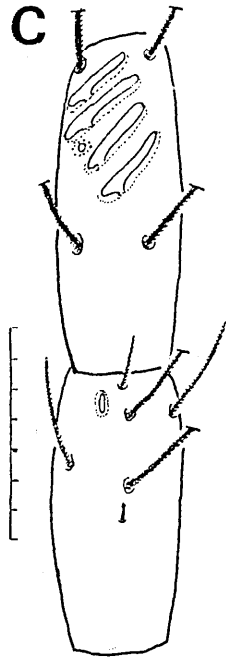
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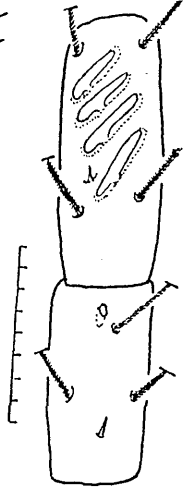
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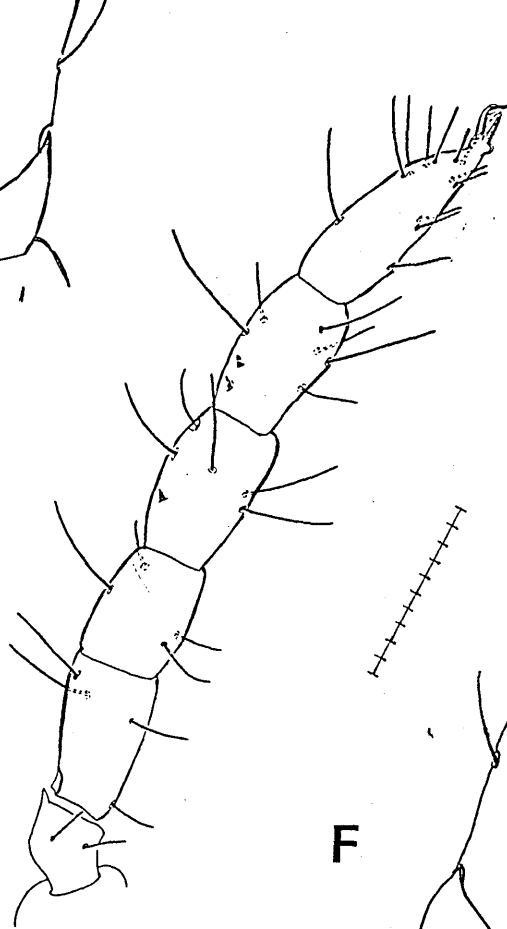
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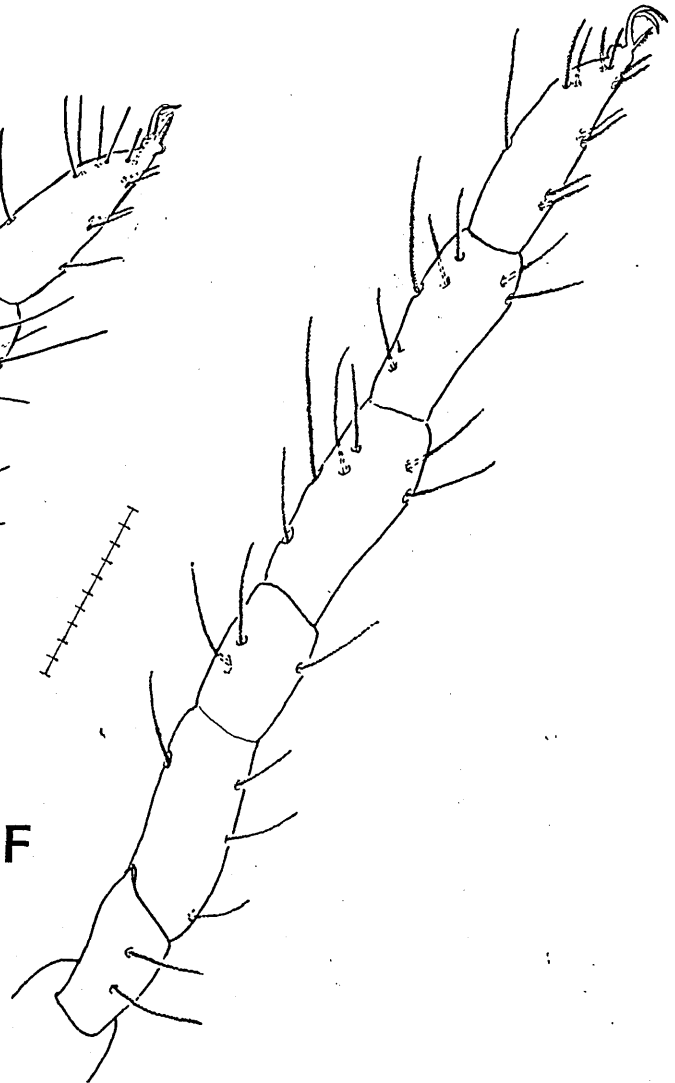
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E



F



Coccorhagidia subterranea (Berlese)

Figs 122 & 123

Rhagidia subterranea Berlese, 1905: 232.*Coccorhagidia berlesei*: Thor & Willmann, 1941: 129.*Coccorhagidia subterranea*: Evans, 1952: 67.*Brevipalpia minima* Zacharda, 1980: 712. n.syn.

DIAGNOSIS. Can be distinguished from other members of the genus by the possession of three rhagidial organs on tarsus I and II and the presence of only one seta on the palp genu.

Body length 348 (329-365), width 122 (107-133).

GNATHOSOMA (Figs 122C,D,E)

Subcapitulum: ratio length to width 1:0.52; malae not clearly differentiated; two pairs adoral setae; subcapitular setae subequal ca. 10 long; two pairs adoral setae.

Palp: setal formula 2-1-9; ω present; tibiotarsus robust, only 1.4 times longer than wide.

Chelicerae: total length 67 (65-68), chela account for approximately one quarter of this; *cha* 5 long, located just proximally to fixed digit; *chb* approximately twice length *cha*, inserted in deep pit just posterolaterally about halfway along fixed digit; digits robust, inner margins smooth; fixed digit narrows suddenly in distal half and terminates in two cusps.

IDIOSOMA - DORSUM (Fig. 122A)

Naso: as for genus.

Setae: (7) clavate, 30 long, stalk accounting for about half length, remainder mostly short, ca. 8, apart from markedly longer scapulars, at 25 long,

other lengths (iv), (c_1), (d_1), (e_1), (f_2), (h_2) subequal, 6-7 long, (ev), (c_2), (f_1), (h_1) 9-11 long.

IDIOSOMA - VENTER (Fig. 122B)

Podosoma: proximal margins of epimeres faintly defined; setal formula 3-1-4-3; lengths 8-9.

Genital area: five pairs short, 6 long, eugenital setae; five pairs genital and aggenital setae, subequal, ca. 8-9 long.

Anal region: (ps_{1-3}) decrease in length from 9-6, (ad_1) 7.

LEGS (Fig. 123)

Robust; I and IV just below two-thirds body length, II and III approximately half body length.

Setae: formulae I 1-10(5+5)-11-11-16, II 1-10(5+5)-5-5-14, III 2-8(4+4)-6-6-12, IV 2-7(3+4)-6-6-12; all shorter than segments.

Solenidia & famuli: tarsi I and II both with three T-shaped rhagidial organs, lying along longitudinal axis of leg; two of those on I in tandem, the third posterolateral to the distal organ, famulus located anterolateral to base of third organ; on II, two organs level and parallel, the third located between them but slightly posterior, famulus not observed; distal rhagidial organ of tibia I with one anterior and one posterior spine associated; that of tibia II with one spine just posterolaterally; tibia III with two adjacent dorso-distal spines; tibia IV with one proximal posterolateral spine; genua I, II, III each with one ventral spine, that of I distal, of II and III approximately medially.

MALE. Unknown.

DISTRIBUTION. Czechoslovakia, England, Scotland, Wales.

MATERIAL EXAMINED. ITALY, Florence, Terriccio di Castagno Giarol. Giapp. (Berlese Coll.) [ISZA, slide no. 79.451. *Brevipalpia minima*, holotype ♀, CZECHOSLOVAKIA, Bohemia centr., Závist-Knoll near Zbraslav, oak forest litter, 27.x.1972, (J. Hlásny) [MZ]. British material: ENGLAND, Devon, Braunton Burrows, slacks between mature dunes, from moss plus underlying 2cm of sand, 7.xii.1981; Torridge Forest, coniferous plantation, in copse separated from forest by 6m of grass, from moss and rotting needles covering rotting branch on floor of copse, 10.xii.1981.

OTHER BRITISH RECORDS. ENGLAND, Bedfordshire, from humus under Sitka Spruce, Corsican Pine and Scots Pine, (G. O. Evans); Kent, Folkestone, The Warrens, grass covered limestone slope, from 7cm of aerial parts of rosebay willowherb and grass plus underlying 1cm of dry soil, 17.iii.1981. SCOTLAND, Fife, Abernethy Forest, from moss amongst *Calluna* at edge of forest, 18.x.1982; Highland, Ben Eighe Moor, from *Polytrichum* moss covering rock by stream. WALES, Dyfed, Tragaron, Cors Tregaron, raised path at edge of bog, by willow swamp, from predominantly club moss plus underlying 1cm of underlying soil on swamp side of path, 24.ii.1981.

Fig. 122. *Caccorhagidia subterranea*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial.

Scale intervals 10 μ m.

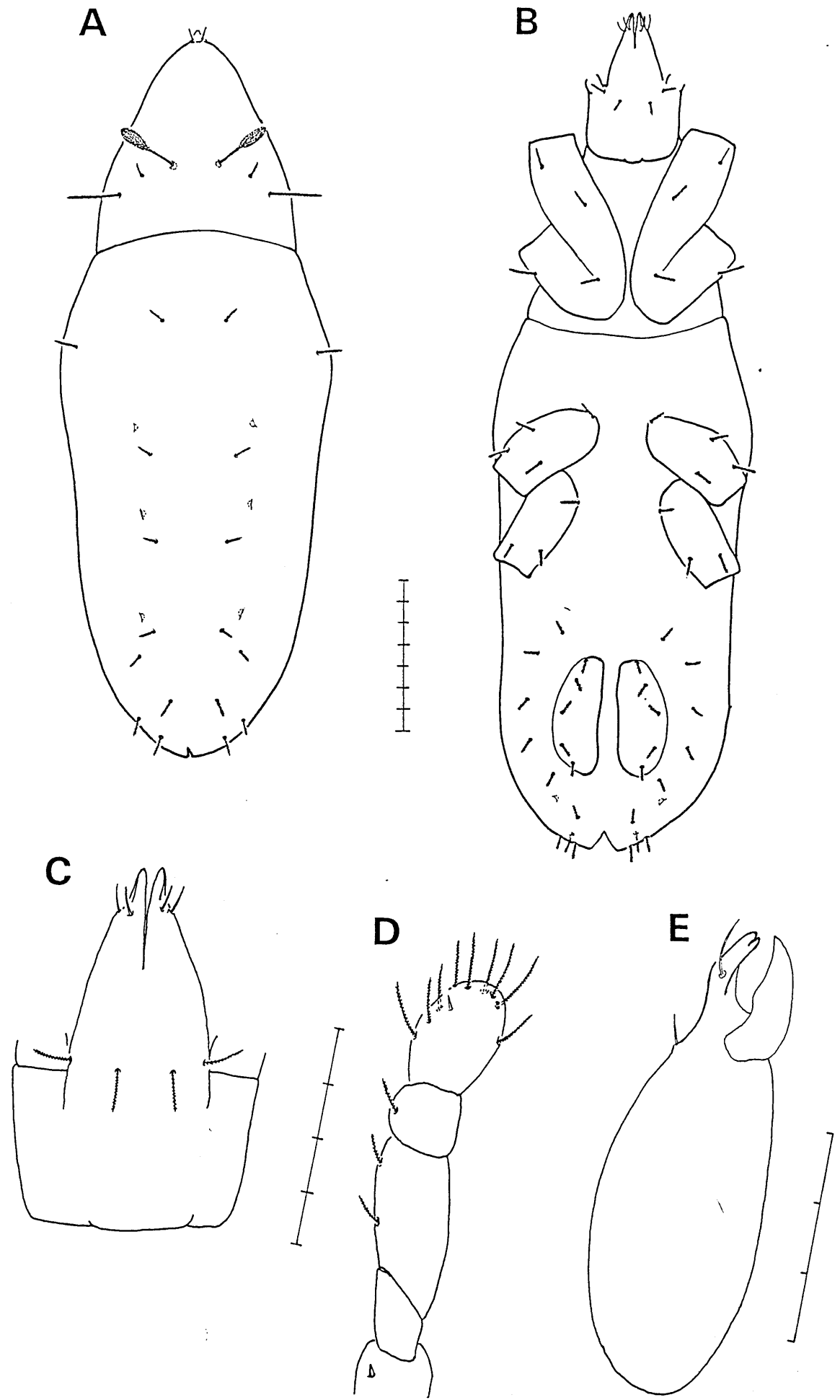
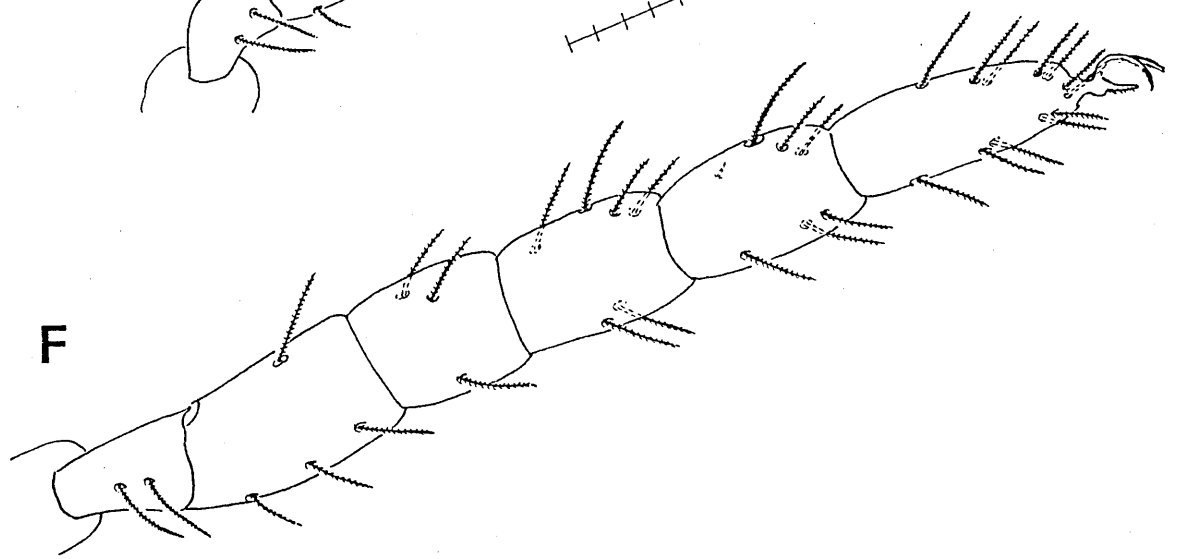
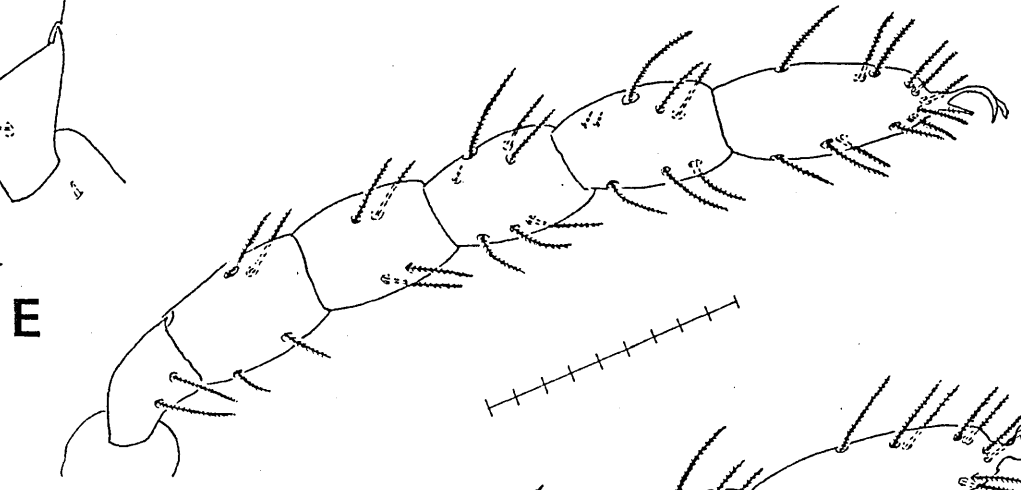
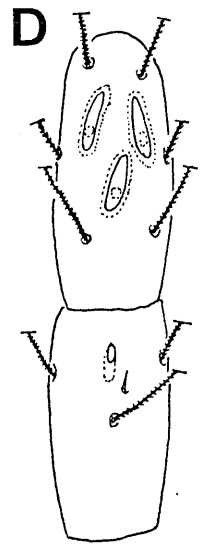
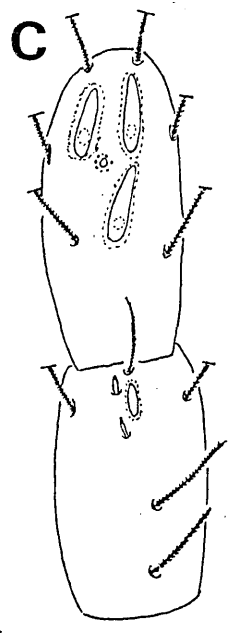
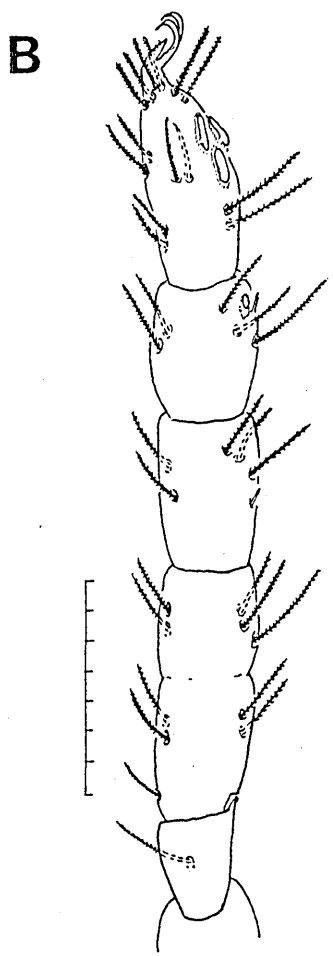
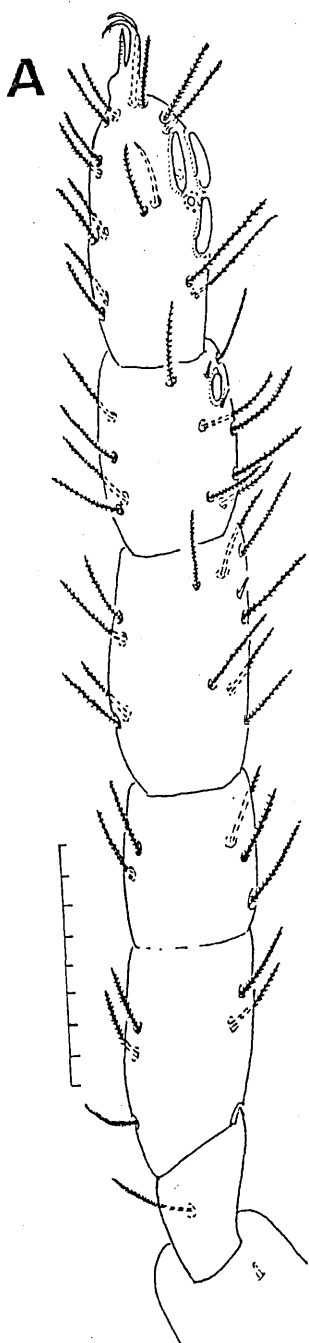


Fig. 123. *Coccorhagidia subterranea*:

- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.



10.1.4.3 Genus *Latoempodia* Zacharda

Latoempodia Zacharda, 1980: 585.

DIAGNOSIS. *Latoempodia* can be distinguished from other rhagidiid genera by the enormously enlarged and elaborate apotele of leg I.

DEFINITION.

Small (435-580).

Chaetome: holotrichous.

GNATHOSOMA.

Subcapitulum: lateral lips membranous, funnel-like; internal and external malae not differentiated.

Palp: setal formula 2-3-9; solenidion present, spiniform; length tibiotarsus ca. twice width.

Chelicera: shaft quite slender; chela account for approximately third of total length; *cha* and *chb* present; movable digit serrated along inner margin.

IDIOSOMA - DORSUM

Naso: rounded triangular peak.

Setae: (*D*) filiform, spiculated conspicuously so in distal two-thirds; remainder short, approximately third intersetal distance.

IDIOSOMA - DORSUM

Podosoma: setal formula 3-1-4-3; setae densely spiculated, tapering.

Genital area: 10 pairs eugenital setae; four or five pairs genital and aggenital setae.

Anal region: as for family.

LEGS.

All shorter than body.

Setae: mostly long.

Solenidia & famuli: rhagidial organs L-shaped; three organs on tarsus I and three or two on tarsus II, arranged more or less parallel in separate pits; famuli not elaborately enlarged.

Apotele: I greatly enlarged, empodium membranous, claws slender.

MALB. Unknown.

TYPE SPECIES. *Latoempodia macroempodiata* Zacharda

DISTRIBUTION. Czechoslovakia, England.

Latoempodia macroempodiata Zacharda

Figs 124 & 125

Latoempodia macroempodiata Zacharda, 1980: 585.New British record

DIAGNOSIS. *L. macroempodiata* can be most easily distinguished from the other species of the genus by the position of cheliceral seta *cha* just proximal to the base of the movable digit and the presence of only two rhagidial organs on tarsus II.

Body length 514 (505-521), width 201 (196-209).

GNATHOSOMA (Figs 124C,D,E)

Subcapitulum: ratio length to width 1:0.6; subcapitular setae *ca.* 26.

Palp: typical for genus.

Chelicera: total length 81 (78-85); *cha ca.* 7 long, located just proximal to base of movable digit; *chb* approximately three times *cha* located just distal to base of movable digit; fixed digit broad in proximal half, then narrows suddenly to point; movable digit only narrows at terminal point, serrated along inner margin.

IDIOSOMA - DORSUM (Fig. 124A)

Setae: lengths (*iv*), (*ev*) subequal, 25 (23-29), (*T*) 71 (68-74), (*sc*) 44 (41-46), (*c*₁), (*d*₁) subequal, 24 (23-26), (*c*₂) 47 (44-49), (*e*₁) 30 (27-32), (*f*₁) 37 (35-39), (*f*₂), (*h*₂) subequal, 27 (25-28), (*h*₁) 48 (45-50).

IDIOSOMA - VENTER (Fig. 124B)

Podosoma: setae *ca.* 26-30 long.

Genital area: five pairs genital and aggenital setae, respectively *ca.* 10 and 18 long.

Anal region: (ps_1) 38(36-41), (ps_2 & s) at 24, approximately third longer than (ad_1).

LEGS. (Fig. 125)

I two-thirds body length, II and III approximately half body length, IV just shorter than I.

Setae: formulae I 1-11(6+5)-8-9-16, II 1-10(5+5)-6-6-14,
III 2-8(4+4)-5-5-12, IV 2-7(4+3)-6-5-11.

Solenidia & famuli: tarsus I with three rhagidial organs in distal half of segment more or less parallel to longitudinal axis of segment, in separate pits, famulus located between median and posterolateral organ; tarsus of II with three rhagidial organs, posterolateral two in tandem and separate pits, the third parallel to distal organ, famulus posterolateral to proximal organ; rhagidial organ of tibia I long, curved, subtended by spiniform solenidion; ventrodiscal spine anterolaterally on tibia II and two medially on anterolateral face of tibia III; rather long ventrodiscal spine respectively antero- and posterolaterally on genua I and II.

Apotela: that of I with much enlarged, membranous empodium and slender claws.

DISTRIBUTION. Czechoslovakia, England.

MATERIAL EXAMINED. Type material: holotype ♀, CZECHOSLOVAKIA, Bohemia, Oblik-Hill near Louny, grassy steppe on western slope, from pitfall trap, 21.iii.1975 (M. Zacharda) [MZ]. British material: ENGLAND, Kent, Folkestone, The Warrens, 300m west along coast path, from thin covering of moss and grass, 17.iii.1981; Suffolk, Hollesley Common, from pine litter, 7.iii.1964 (P.N. & K. Lawrence); Hollesley Common, from birch and conifer litter, 7.iii.1964 (P.N. & K. Lawrence).

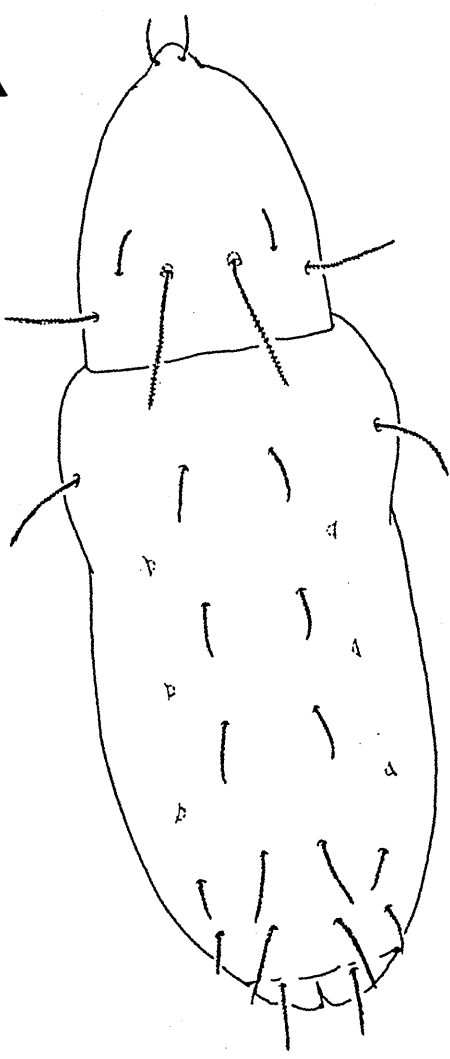
REMARKS. *L. macroempodiata* was an uncommon species, found only from the above localities.

Fig. 124. *Latoempodia macroempodiata*:

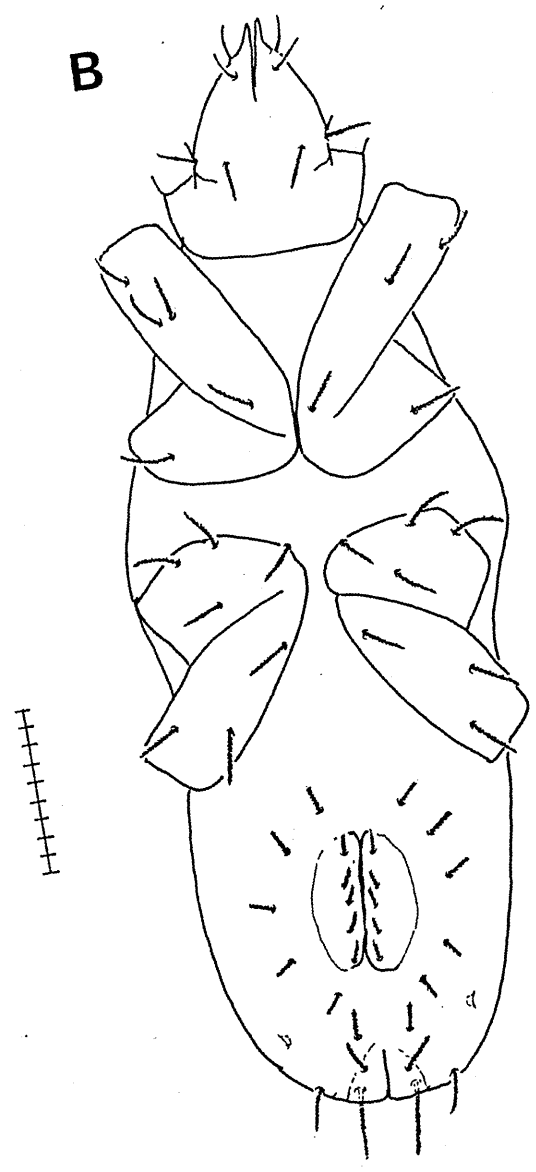
- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial.

Scale intervals 10 μ m.

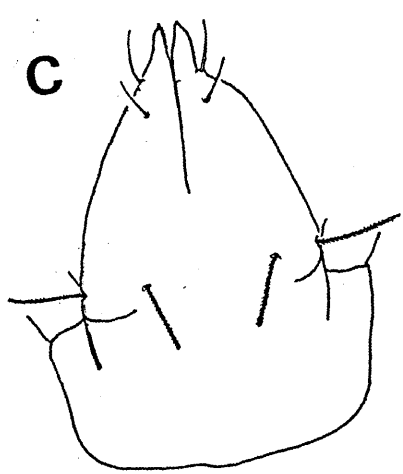
A



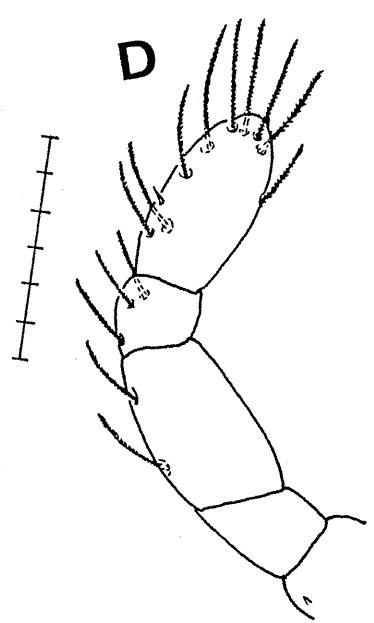
B



C



D



E

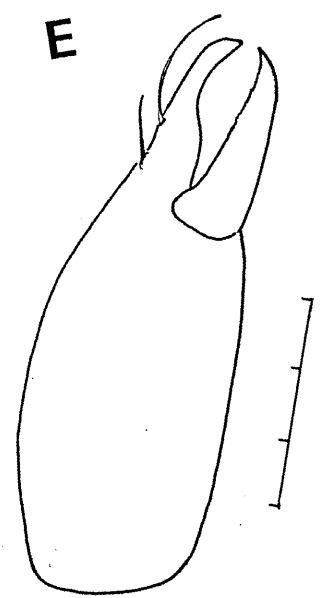
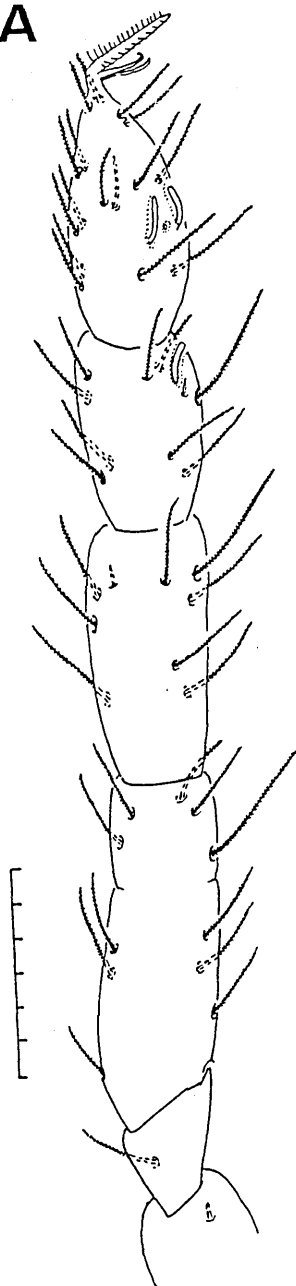


Fig. 125. *Latoempodia macroempodiata*:

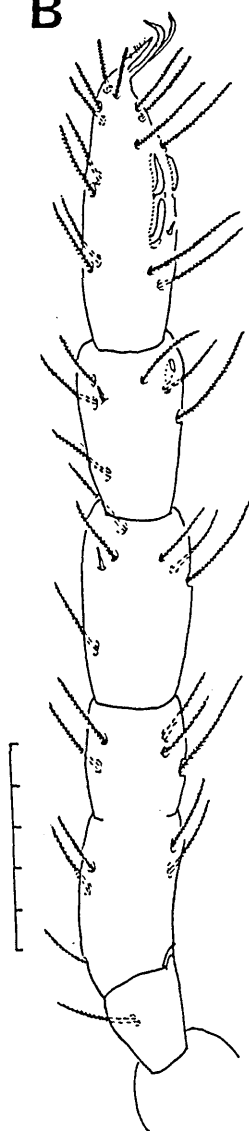
- (A) leg I, posterolateral;
- (B) leg II, posterolateral;
- (C) tarsus & tibia I, dorsal;
- (D) tarsus & tibia II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral.

Scale intervals 10 μ m.

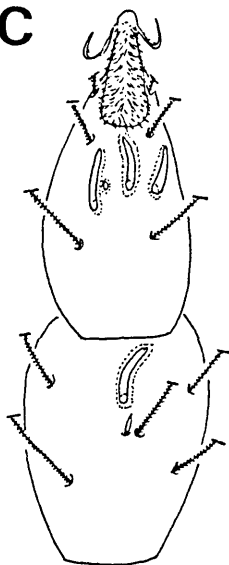
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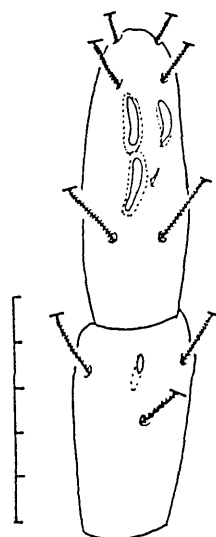
B



C



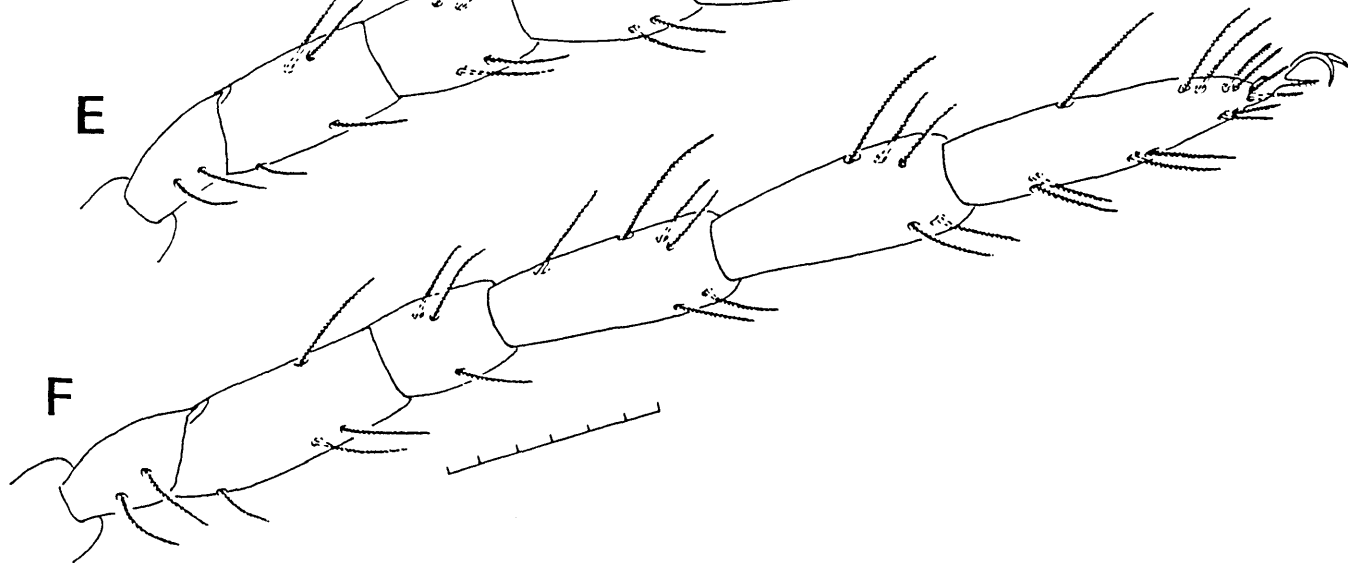
D



E



F



10.1.4.4 Genus *Shibaia* Zacharda

Shibaia Zacharda, 1980: 737.

DIAGNOSIS. *Shibaia* can be distinguished from the other genera of the family by the rhagidial organs of tarsus I arranged parallel to each other and to the longitudinal axis of the segment, the stalked famulus I located distally to the rhagidial organs and the occurrence of rhagidial organs on most leg segments.

DEFINITION.

Small to large (500-1200).

Chaetome: holotrichous or hypotrichous.

GNATHOSOMA.

Subcapitulum: internal and external malae differentiated, more or less acuminate; two pairs adoral setae.

Palp: formula 2-3-10; length tibiotalrus 1.5 times width; solenidion present, spiniform.

Chelicera: shaft slender; chelate portion account for approximately quarter total length; fixed digit terminates in two cusps; movable digit serrated; *chb* absent.

IDIOSOMA - DORSUM

Naso: rounded triangular.

Setae: (*T*) spiculated, particularly so in distal two-thirds; remainder half to three-quarters intersetal length, densely spiculated, tapering; if hypotrichy occurs, (*f*₁) is absent.

Lyrifissures: as for family.

IDIOSOMA - VENTER

Podosoma: setal formula 3-1-4-3; setae desnsely spiculated, tapering.

Genital area: five or nine pairs eugenital setae; five pairs both genital and aggenital setae, densely spiculated.

Anal region: as for family.

LEGS.

I shorter or just longer than body.

Setae: long, densely spiculated.

Solenidia & famuli: rhagidial organs T-shaped; tarsus I with four or five rhagidial organs, famulus with long stalk, located distally to organs; tarsus II with two or five rhagidial organs, famulus absent; rhagidial organs present on other leg segments, apparently in place of erect spiniform solenidia.

Apotela: all of similar form, although empodium of I is shorter than claws.

MALE. Sperm sac as for family.

TYPE SPECIES. *Rhagidia heteropoda* (Berlese).

DISTRIBUTION. Czechoslovakia, Austria, Alaska, Hawaii, South Korea.

Shibaia heteropoda (Berlese) n.comb.

Figs 17d, 126 & 127

Rhagidia heteropoda Berlese, 1910: 243.*Rhagidia longisensilla* Shiba, 1969: 79, n.syn.*Rhagidia longisensilla*: Strandtmann, 1971: 104; Baltac, 1974: 41;

Strandtmann & Goff, 1978: 135.

Shibaia longisensilla: Zacharda, 1980: 738.New British record

DIAGNOSIS. This species can be distinguished from the other members of *Shibaia* by the four long rhagidial organs of tarsus I, occupying approximately half the segment in combination with its relatively small size.

Body length 497 (480-524), width 190 (185-203).

GNATHOSOMA (Figs 126C,D,E)

Subcapitulum: ratio length to width 1:0.5; internal malae needle-like; external malae not differentiated; subcapitular setae 35 (32-37).

Palp: as for genus.Chelicera: total length 141 (137-146); *cha* ca. 23 long.

IDIOSOMA - DORSUM (Fig. 126A)

Nasq: roughly triangular protrusion of prodorsum.

Setae: (*f*₂) absent; (*sc*) and (*c*₂) markedly longer than other setae; lengths - (*iv*) 37 (34-42), (*ev*) 34 (30-37), (*T*) 139 (133-146), (*sc*) 119 (111-123), (*c*₁) 39 (35-44), (*c*₂) 96 (89-103), (*d*₁) 39 (35-43),

(e₁) 42(37-45), (f₁) 70(67-74), (h₁) 69(66-74), (h₂) 32(29-35).

IDIOSOMA - VENTER (Fig. 126B)

Podosoma: (a) setae ca. 20 long, approximately third to half length of other setae.

Genital area: nine pairs eugenital setae, subequal ca. 9 long; five pairs genital setae, subequal ca. 13; five pairs aggenital setae, subequal ca. 25 long.

Anal region: (ps₁) 61(57-66), (ps₂ & 3) and (ad₁) subequal, ca. 32 long.

LEGS (Figs 17d, 127)

I and IV approximately three-quarters body length, II and III just over half body length.

Setae: formulae I 1-11(6+5)-10-10-20, II 1-11(6+5)-8-7-18

III 2-8(4+4)-6-6-16, IV 2-6(3+3)-6-5-16.

Solenidia & famuli: tarsus I with four level rhagidial organs parallel to longitudinal axis of segment dorsally, anter- and posterolaterally on distal half of segment; famulus with greatly elongated stalk, located distally to median organs just behind apotele; tarsus II with two rhagidial organs in tandem and confluent pits dorsally on median third of segment; tibia I with two dorsal organs, proximally and distally; tibiae II and III with two obliquely parallel organs dorsally on proximal half of segment, II with a third organ ventrally; tibia IV with one rhagidial organ dorsally on proximal half of segment; genua I and II with organ ventrally on posterolateral face; genua III and IV with one organ dorsomedially; spiniform solenidia absent.

DISTRIBUTION. Czechoslovakia, Eire, England, Hawaii, Italy, Rumania, Scotland, Wales.

MATERIAL EXAMINED. Type material: ITALY, Toiano, from moss [ISZA, slide no. 88/46]. British material: ENGLAND, Surrey, near Dorking, Box Hill, Happy Valley, from surface sample of grass, vii.1984.

OTHER BRITISH RECORDS. EIRE, Galway, moss, turf, lichen *etc* by bog, 27.vi-10.vii.1971 (P.N. Lawrence). ENGLAND, Kent, Dungeness, shingle area around power station with patches of gorse, broom, grass, moss and lichens, from grass under gorse plus top 1cm of moist soil, 18.3.1981; Cheshire, Ellesmere Port, arable land by Sycamore Park, from aerial parts of grass plus roots in underlying 4cm of soil, 26.ii.1982; Suffolk, 2km SW of Walberswick, Dingle Great Hill, midway on west slope, from grass plus top 1cm of underlying soil, 7.i.1981. SCOTLAND, Strathclyde, western shore of Loch Lomond by Edrich Water, from litter in hollow at ground level of willow tree, 12.ix.1982; Fife, Abernethy Forest, from pine litter, 18.ix.1982. WALES, Dyfed, Rheidol Forest, from top 4cm of soil under bracken in clearing amongst hemlock approximately 30m from edge of forest, 25.ii.1981.

REMARKS. Unfortunately, the type material of *Rhagidia longisensilla* was not made available to me, but Shiba's description and figures (Shiba 1969) provide sufficient details to allow the above synonymy.

Fig. 126. *Shibala heteropoda*:

- (A) idiosoma, dorsum;
- (B) idiosoma, venter;
- (C) subcapitulum, venter;
- (D) palp, antiaxial;
- (E) chelicera, antiaxial.

Scale intervals 10 μ m.

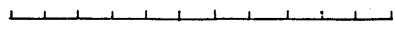
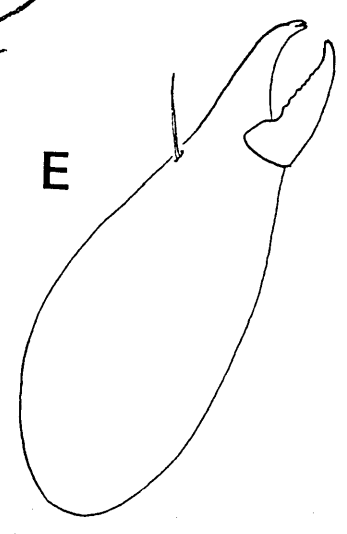
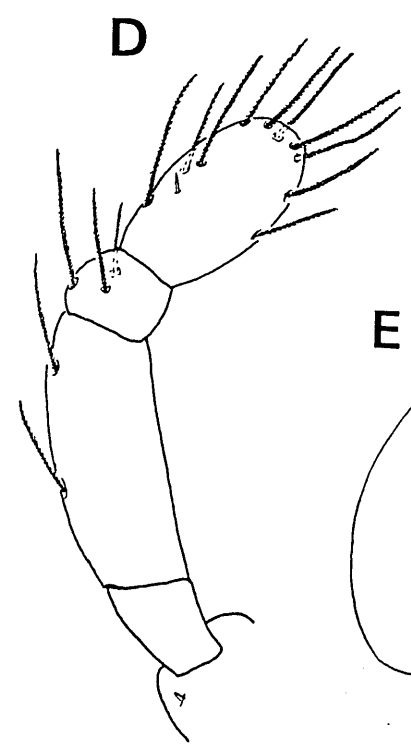
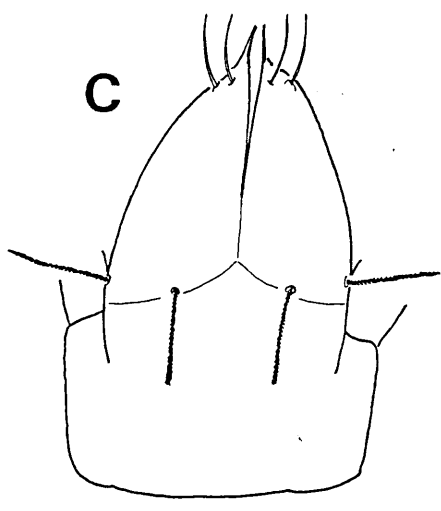
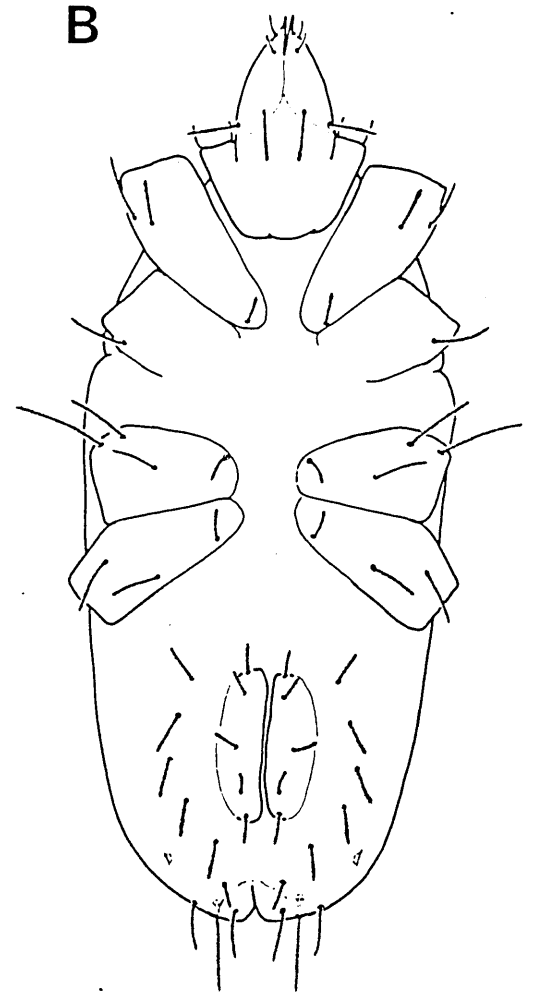
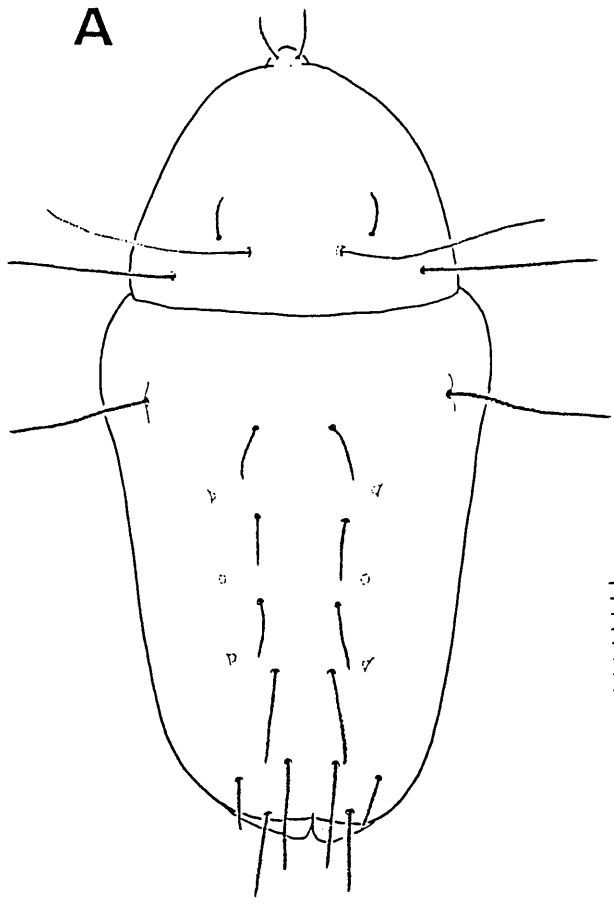
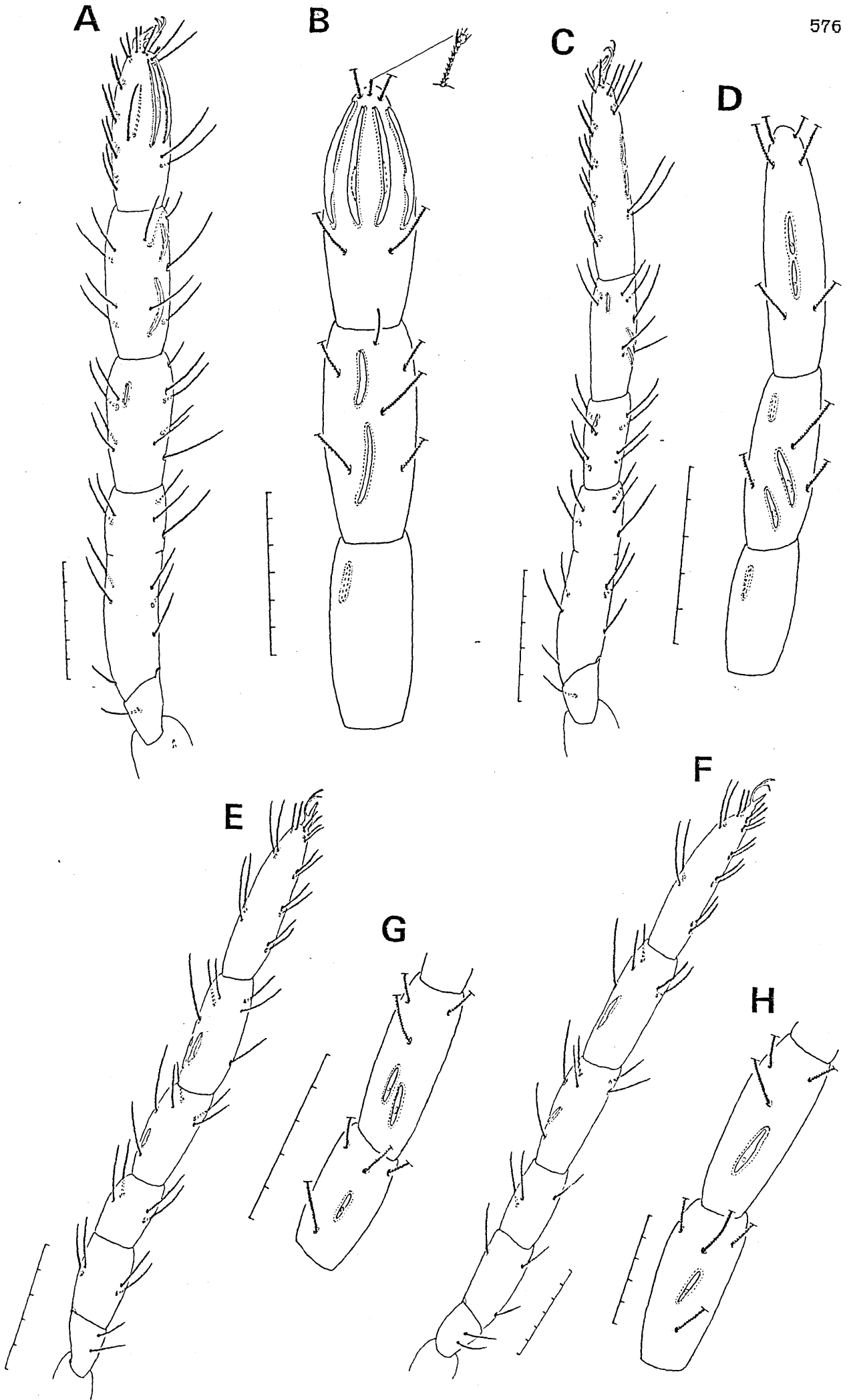


Fig. 127. *Shibaia heteropoda*:

- (A) leg I, posterolateral;
- (B) tarsus, tibia & genu I, dorsal with famulus enlarged;
- (C) leg II, posterolateral;
- (D) tarsus, tibia & genu II, dorsal;
- (E) leg III, anterolateral;
- (F) leg IV, anterolateral;
- (G) tibia & genu III, dorsal;
- (H) tibia & genu IV, dorsal.

Scale intervals 10 μ m.



11. ONTOGENETIC DEVELOPMENT OF THE IDIOSOMA

11.1 INTRODUCTION

To date, few details concerning eupodoid ontogeny have been published; available data being limited to Ehrnsberger's comparative study of prelarvae (Ehrnsberger 1974) and to the description of immature stages of certain species (Pittard 1971, Strandtmann 1971, Gless 1972, Coineau 1976). Material obtained during the course of the present study, however, afforded the opportunity to study aspects of ontogeny in several taxa.

The discovery of *Caleupodes reticulatus*, which possesses external evidence of primary opisthosomal segmentation, facilitated the interpretation of the association between idiosomal segments, setae and lyrifissures (Baker, A.S. in press), while the examination of all active life stages of five species (see below for details), enabled the sequence of setal addition to be observed. Furthermore, conclusions drawn from the above studies, together with data obtained from the examination of the larva of *Penthaleus minor*, enabled certain observations to be made concerning the neotrichous chaetome of members of the Penthaleidae.

Information obtained from an ontogenetic study can be used to assess differences between the respective immature stages of various taxa and also to identify homologous structures in other acarine taxa. The latter has a two-fold application as, with homologies established, it may provide data on relationships between taxa and it also enables taxa to be more easily compared. The present study is somewhat exploratory in nature since only a small number of species is included, but it was hoped that the data obtained would reveal trends in the ontogenetic development of eupodoids.

The following account describes the ontogeny of the idiosoma, gnathosoma and leg solenidia only, since it was not possible to resolve any pattern of setal addition in the legs at supra-specific level.

The results are largely discussed in terms of the work of Grandjean who recognised the ordered ontogenetic sequence in which segments and integumentary structures (setae, solenidia and lyrifissures) appear. Grandjean also devised standardized notation systems for homologous organs; this work is described in a series of papers between 1935 and 1961. As noted in Section 7.3.1, the Eupodoidea have acquired their own system of setal designation; largely that devised by Strandtmann (1967, 1971). It would, however, allow easier discussion if homologous structures of the various acarine taxa carried the same notations. Consequently, and following the example of other authors who have successfully applied Grandjean's notations to a variety of acariform taxa (Knülle 1959, van der Hammen 1969, Lindquist 1977, Quiros-Gonzalez & Baker 1984) the system is applied to the Eupodoidea.

11.2 SPECIES STUDIED

During the course of the present study, material was extracted from isolated habitats, such as tree-holes, which comprised immatures plus only one or a small number of different adults. In the former instance, unless association was clearly unlikely, for example, if the form of the trichobothria differed or the immature stages were larger than the adults, the different stages were assumed to be linked. Similarly, in certain of those samples containing only a few adult species, associations could be determined by a process of elimination. It was possible to match all four active immature stages to the respective adult

of three species of eupodid (*Alloeupodes interruptus*, *Cocceupodes trisetatus* and *Eupodes alaskanensis*) and to one rhagidiid (*Rhagidia clavicornita*).

Unfortunately, no immature stages of *Penthalodes*, the only British member of the family Penthalodidae, were found and so, to make the study more complete, data from the study of *Stereotydeus mollis* by Pittard (1971) is included, supplemented by personal observations of certain of the stages.

In addition, the larva of *Penthaleus minor* was identified and included as it was hoped that the chaetotaxy of this stage would reveal information concerning the adult condition.

In the following account, the development of each part of the body will be discussed in turn.

11.3 ONTOGENY OF THE EUPODOIDEA

Gnathosoma

Apart from in the larval *P. minor*, where the holotrichous condition occurs in the palp femur and genu, all setae on the gnathosoma were present throughout ontogeny.

Prodorsum

Grandjean (1933, 1939, 1939b) proposed the primitive condition of six pairs of prodorsal setae, the number remaining constant throughout ontogeny. In the Eupodoidea, there are normally four pairs, although three and five are, respectively, found in *Eupodes strandtmanni* and members of the genus *Pilorhagidia*. It is difficult to homologise these

setae with those of other taxa and so the designations used by Strandtmann (1967, 1971) are retained.

In the adults of most neotrichous taxa, more than four pairs of setae occur, while a number of unpaired ones are also often present. Consequently, apart from the internal verticals and trichobothria, it is not possible to identify either the number or position of the other pairs of prodorsal setae. Observations of the larval *P. minor*, however, demonstrate that the holotrichous complement of four pairs of setae is, indeed, present (Fig. 130).

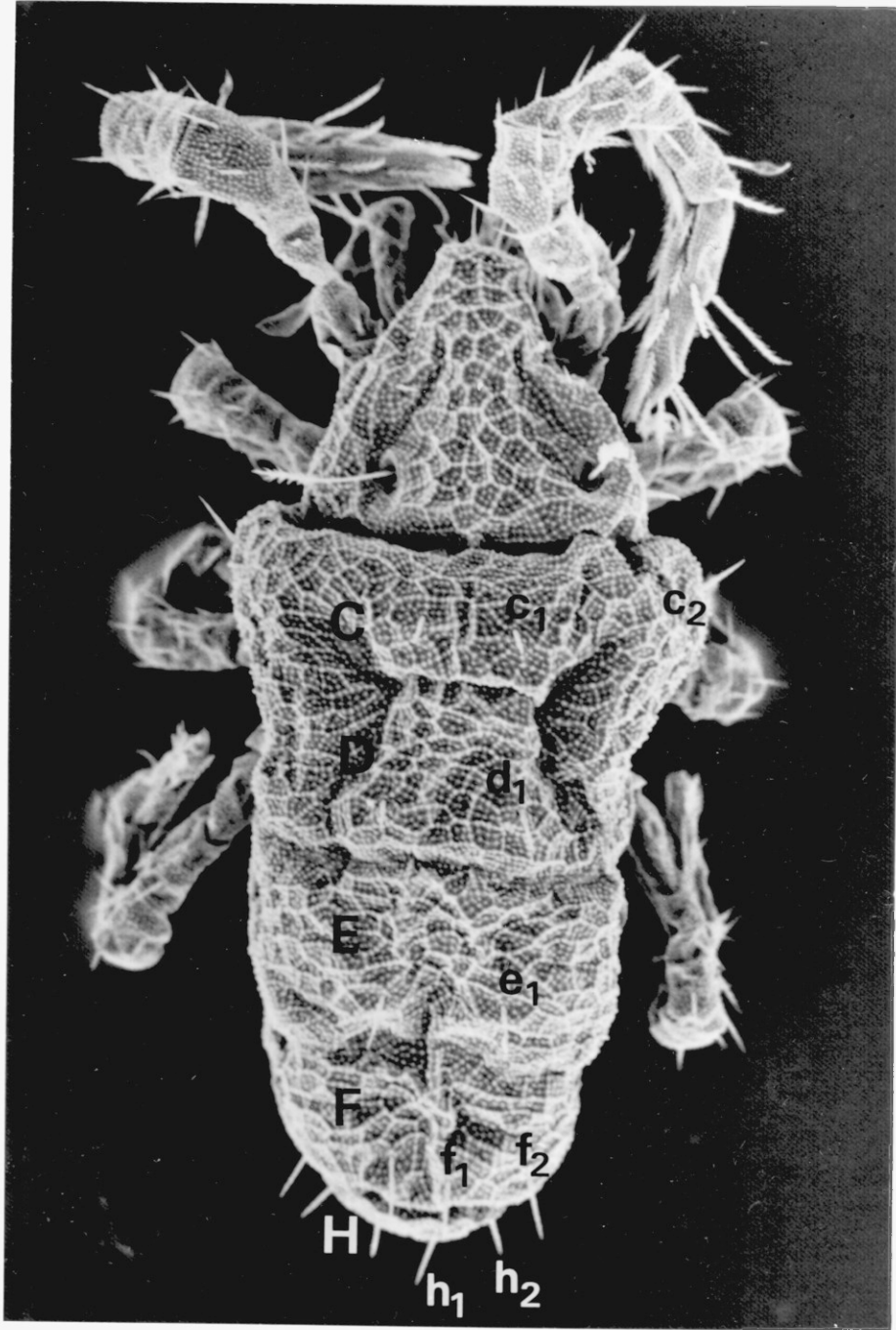
Opisthosoma

Grandjean (1954) postulated that the primitive acariform larva possesses six opisthosomal segments, or five segments and a telson (Anderson 1973, Aeschlimann & Hess 1984), each carrying one pair of lyrifissures (=cupules, slit-organs) and four pairs of setae on the dorsal and lateral surfaces. With each moult a similar segment is added posteriorly. Coxal and genital setae are added during ontogeny but it is only possible to identify at which stage they arise and not to which segment they belong.

In the Eupodoidea, the usual adult complement of eight pairs of dorsal setae are arranged in five transverse rows while two, three or four pairs are associated with the anus. Three pairs of lyrifissures are present dorsally and one ventrally but, hitherto, their association with setae and segments has been difficult to determine.

C. reticulatus possesses external evidence of primary segmentation; transverse furrows of differentiated integument (Fig. 128) are taken to indicate the limits of the segments and are used to interpret both the number of segments and the association between segments, setae and lyrifissures. Seven segments were identified in the adult.

Fig. 128. *Caleupodes reticulatus*: illustrating the application of Grandjean's (1947) notation system for opisthosomal segments, setae and lyrifissures.



Applying Grandjean's (1947) notation system the segments are, from anterior to posterior, C, D, F, H, PS (pseudanal) and AD (adanal). The segmental boundaries demonstrate that lyrifissures *ia*, *im*, and *ip* are located respectively on segments D, E and F, while *ih* is situated ventrally on segment H. Segments D and E both possess a single pair of setae while C, F, H and PS all carry two pairs. The anus, therefore, opens onto the adanal segment, which is devoid of setae and lyrifissures, so making the pseudanals the most posterior.

Unfortunately, attempts to collect immature stages of *C. reticulatus*, particularly the larvae, were unsuccessful and so it is not possible to record the ontogenetic development of this species. The above observations of the adult *C. reticulatus* combined with data from the species examined in this study, however, indicate that, in the superfamily Eupodoidea, a seventh segment is indeed added at the protonymphal stage.

Three sequences of segmental and setal addition were observed and are schematically represented in Fig. 129. The first two are similar, only differing in the number of pseudanal setae present. Larvae of the families Eupodidae and Penthlodidae possess the adult complement of setae associated with the anus, i.e. two or three pairs of pseudanal setae. These setae are located on the anal flaps, while lyrifissure *ih* occurs close to the junction of the anal flaps and the surrounding integument. Pittard (1971) figures the pseudanal setae of *S. mollis* to surround the anal flaps but personal observations confirmed their presence on the flaps themselves. The terminal larval segment onto which the anus opens is, therefore, regarded to be the pseudanal. In the protonymphal stage, the anal flaps are nude, the setae and lyrifissures now being located on the integument surrounding the anus.

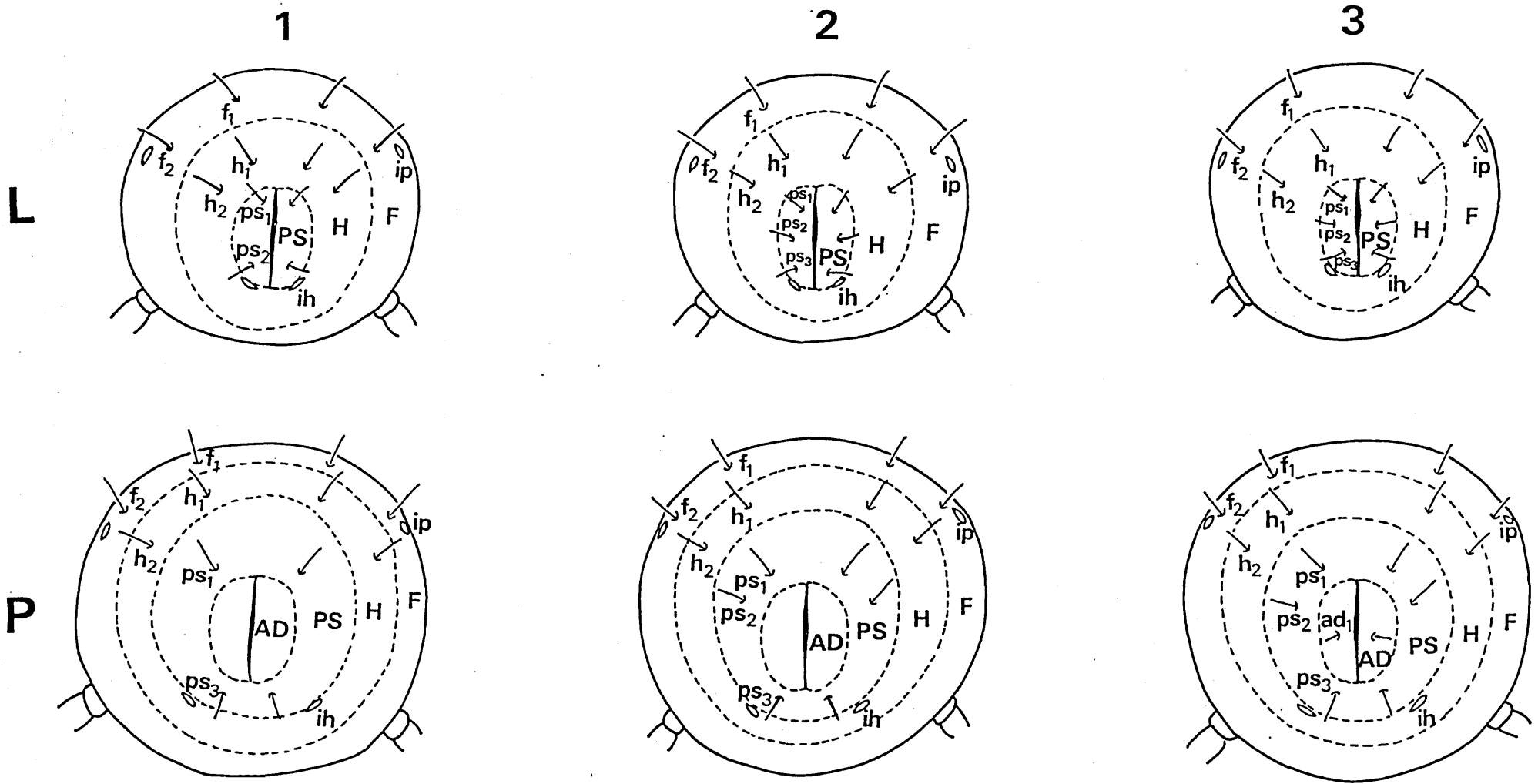


Fig. 129. Ontogenetic development: Posterior view of larvae (L) and protonymph (P) illustrating the three schemes of segmental and setal addition.

This is interpreted as the addition of a seventh, the adanal, segment, onto which the anus now opens.

The third scheme applies to the family Rhagidiidae. It has been stated that no setae are added postlarvally in the Rhagidiidae (Zacharda 1980). In the larval rhagidiids here examined, only three pairs of setae were observed to be associated with the anus and these were located on the anal flaps, *i.e.* the pseudanal segment. Again, lyrifissures *lh* occur just anteriorly to the junction of the anal flaps and surrounding integument. As in the schemes described above, the three setae in protonymphal rhagidiids are located on the integument surrounding the anus but a fourth pair has appeared, positioned on the anal flaps. The setae of this fourth pair, occurring as they do on the adanal segment, are consequently regarded as adanal setae.

In the larval *P. minor*, the chaetome is reduced to the holotrichous condition while the anus now occupies a terminal and not dorsal position. This situation enables the homologues of the setae and lyrifissures of holotrichous eupodoids to be identified (Fig. 130).

Podosoma (Fig. 131)

Grandjean's (1935) system of notation can be applied to the setae of the podosoma of eupodoids.

In the representatives of all four families, the larval setal complement is $2(1a \ \& \ b)-1(2b)-2(3a \ \& \ b)$. At the protonymphal stage, coxa I has the full complement of setae, while 3c is also added. Coxa IV is present at this stage but is devoid of setae.

In the deutonymph, *A. interruptus*, *E. alaskanensis*, *R. clavicrinita* and

Stereotydeus mollis, i.e. those taxa with more than three setae on coxa III, seta 3d is added, while setae 4a and 4b are added in all taxa.

In the tritonymph, all taxa possess the adult complement of setae.

Genital area (Fig. 131)

As described in Section 7.3.9, external evidence of genitalia appears at the protonymphal stage, while internal genital setae only occur in the adult. In all taxa examined in this study, the protonymphal and deutonymphal genital setation comprises, respectively, one pair of genital setae and two pairs of both genital and aggenital setae. *S. mollis*, however, is an exception in possessing only one pair of aggenitals in the protonymph. The two stages also, respectively, possess one and two pairs of genital papillae.

In the tritonymph, some variation between taxa occurs. In the eupodid species, there are three pairs of genital setae and a variable number of aggenitals. In *A. interruptus* and *C. trisetatus*, there are just three pairs whereas *E. alaskanensis* possesses five. *S. mollis* possesses respectively three and four pairs of genital and aggenital setae.

In the Rhagidiidae, available evidence suggests that those species with six pairs of genital setae as adults (e.g. *R. clavicrinita*) possess four pairs of aggenitals in the tritonymphal stage, while those with five as adults have only three pairs as tritonymphs.

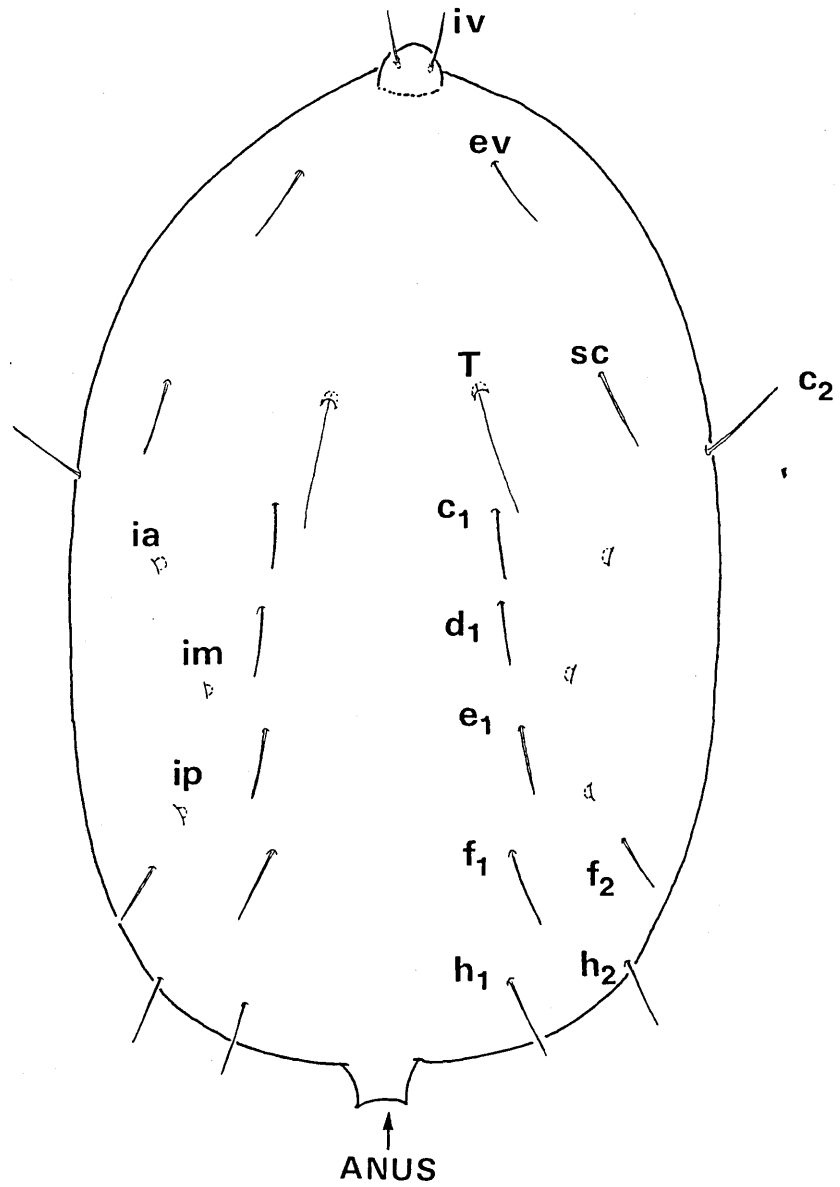


Fig. 130. *Penthaleus minor*, dorsum of larva.

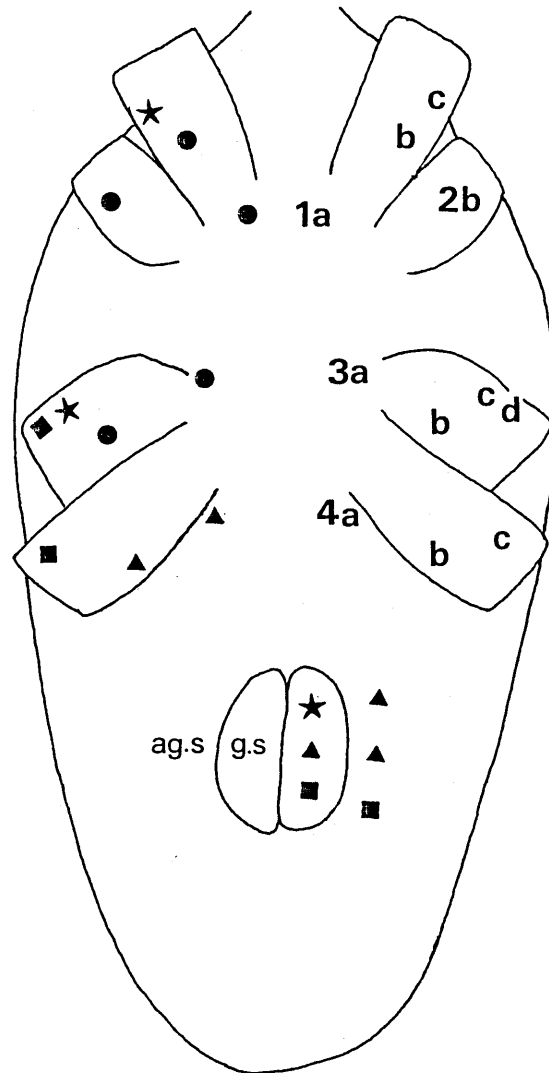


Fig. 131. Ontogenetic development: illustrating setal addition in the podosomal and genital areas.

Leg solenidia and famuli

The same sequence of addition was seen in all species studied. Genual and tibial complements are present from the larval stage. One rhagidial organ and the famulus occur on the larval tarsi I and II and remains unchanged until the deutonymph. A further organ is added at this stage and, depending on the adult complement, at all subsequent stages.

11.4 REMARKS

Contrary to the statement by Kethley (1982) that no addition occurs in eupodoids past the pseudanal segment, the above study is considered to have demonstrated the addition of the adanal segment. Furthermore, the anal flaps of rhagidiids were shown not to be devoid of setae, but, in fact, to carry a pair of adanals. The latter were previously considered to be part of the pseudanal row.

Setal addition to the podosoma and genital region and solenidial addition to the legs follow a set order, variations apparently being dependant on the adult complement and not on the identity of the taxon.

Ontogenetic knowledge of related acarine taxa is scanty although the account of the Tydeidae given by André (1979, 1981, 1981a) provides further evidence for their close relationship with the Eupodoidea. André presents convincing data for the postlarval addition of the adanal segment but he concludes that it is not experimentally supported.

The complement of podosomal setae is the same in both larval tydeids and eupodoids and exhibit similar sequences of setal addition. Tydeids, however, show a greater variety in the order of appearance of aggenital and genital setae, although this is likely to be attributable to the relatively smaller number of eupodoids examined.

In the Tydeidae, the solenidia and famuli of the legs are all present at the larval stage. Interestingly, this solenidial complement is the same as occurs in larval eupodoids.

12. SUMMARY

1. A collection of British eupodoid mites was made. The methods of collection, extraction and preparation for study are described.
2. The major taxonomic literature concerning the superfamily is reviewed.
3. Based predominantly on material from the above collection, a study of the external morphology of eupodoid mites was made. Scanning electron micrographs are used to illustrate structures, some for the first time. The study revealed a number of new characters and revised certain observations made previously by other authors. These are:
 - a) Claparède organs occur in the larval stage.
 - b) only two pairs of genital papillae are ever found.
 - c) the sperm sac of males can be either unornamented and subclavate or with reticulate patterning and capitate.
 - d) although sometimes difficult to discern, four pairs of idiosomal lyrifissures are present.
 - e) segmental addition occurs postlarvally (see item 9 below).
 - f) two pairs of adoral setae occur in the families Eupodidae, Penthaleidae and Penthalodidae as well as in the Rhagidiidae.
 - g) the 'solenidion' of tarsus II (Kethley 1982) is identified as the famulus.
 - h) the proximal solenidion on tibia II of eupodids can be erect or rhagidiform.
 - i) a famulus is present on tibia I of eupodids and penthaleids.
 - j) a distal papilla occurs on the leg genua in the families Penthaleidae and Penthalodidae.
 - k) the palp femur carries two setae in the Penthalodidae.

- l) nine setae occur on the palp tibia-tarsus of members of the families Eupodidae, Penthaleidae and Penthaleodidae; *l'* being spiralled.
 - m) the ornamentation of penthalodids can be other than pentagonal.
 - n) the chaetome in *Penthalodes* is hypotrichous, the *h* row being absent.
 - o) the chelicera is devoid of setae in the genus *Penthalodes*.
 - p) the anus is normally subterminal in penthalodids.
 - q) the number of palp femoral setae in adult penthaleids varies.
 - r) the normal complement of lyrifissures can be discerned in the Penthaleidae.
 - s) the four pairs of setae in the anal region of rhagidiids are interpreted as three pairs of pseudanals and one pair of adanals.
 - t) the idiosomal chaetome in rhagidiids is normal, hypotrichous or neutrichous.
 - u) the genus *Pilorhagidia* possesses three pairs of pseudanal setae and one pair of adanals.
4. A phenetic analysis was carried out on the British species collected at the beginning of the study (apart from one found subsequently) plus representative examples of genera not found in Britain. A data set of 90 characters, describing all aspects of external morphology, was used. The method failed to satisfactorily indicate familial groupings but enabled clusters indicating genera in the families Eupodidae, Penthaleodidae and Penthaleidae to be identified. The analysis also failed to divide the majority of the members of the family Rhagidiidae which formed a large diffuse cloud with no subgroupings. It was concluded that the influence of qualitative and large numbers of primitive characters can overshadow systematically more important features.

5. A cladistic analysis was carried out on the taxa included in the phenetic study (plus one British species found subsequently) and using most of the same characters. The superfamily Tydecoidea was established as the sister-group of the Eupodoidea and utilized as its out-group for polarizing the majority of the characters, functional out-groups being used to resolve the remainder. The Eupodoidea was demonstrated to be a holophyletic group. Initially, four monophyletic groups were identified within the superfamily which represented the families Eupodidae, Penthaleidae, Penthaleodidae and Rhagidiidae. The members of each family fell into holophyletic groupings representing genera although, again, this was less satisfactory in the Rhagidiidae.

6. A discussion of systematic methods concluded that, of phenetics and cladistics, the latter produced the more valid classification. While, by altering the data set, phenetic analyses will produce clustering in OTUs, the resulting groupings are not invariably natural. In the cladistic approach, systematically important characters are not overshadowed by a mass of irrelevant ones. Since, however, any systematic method depends on the character choice made by the worker, the contribution of his/her judgement cannot be discounted.

7. A revised supra-specific classification, based on the cladistic analysis, is proposed. The taxa are classified into four families, four new eupodid genera are described, while 13 of the rhagidiid genera described by Zacharda (1980) are declared invalid. The diagnoses and definitions of previously established taxa are amended and more consistent use is made of defining characters.

8. The adults of the 40 species found in the British fauna are diagnosed, defined and figured. Ten species are new to science and 19 new to the British fauna. Three new synonymies and 10 new combinations

are proposed, while three species revert to their original genus. A new type species for the genus *Eupodes* is designated while the date of establishment of two others is clarified. Identification keys to the families and genera of the world and to the British species are provided.

9. A preliminary study of ontogenetic development provided the following information:

- a) the interpretation of the association between opisthosomal segments, setae and lyrifissures, facilitated by the discovery of *Caleupodes reticulatus*, enabled homologues to be identified in other acarine taxa and, hence, the application of Grandjean's notation system (Grandjean 1947).
- b) one segment, the adanal, is added at the protonymphal stage.
- c) there is no postlarval setal addition to the gnathosoma.
- d) larvae of the families Eupodidae and Penthelodidae possess a complete set of idiosomal and pseudanal setae and lyrifissures.
- e) one pair of adanal setae is added to the protonymph of members of the family Rhagidiidae.
- f) for all taxa examined, the larval and protonymphal setation of the podosoma is the same. In the deutonymph, differences in addition only occur on coxa III and depends on the number of setae which occur in the adult. The adult complement is present at the tritonymphal stage.
- g) with the exception of one of the species examined, the setal complement of the genital region is the same in the respective proto- and deutonymphal stages. In the tritonymph, the number of genital setae is constant but that of the aggenitals varies.
- h) the full solenidial complement of the leg genua and tibiae is present in the larva, while, on the tarsi, only one plus the

famulus occurs. The remainder of the tarsal solenidia are added after the protonymphal stage.

- i) the holotrichous chaetome of the larval *Pentbaleus minor* reveals the presence of three pseudanal setae.

10. During the course of the project, two main areas for further research were identified:

- a) the reassessment of the classification of the taxa of the family Rhagidiidae, including all known species and using a reconsidered data set.
- b) the study of the ontogeny of many more species in order to confirm trends of setal addition identified here and to obtain more information on the addition of leg setae.

11. Based on parts of the above work, two papers have been prepared for publication (Baker, A.S. 1985, Baker A.S. in press).

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14. APPENDICES

APPENDIX I. Run 1 of phenetic analysis - nearest neighbours list.

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
1	59	99	8	60	97
	4	97		7	97
	29	89		62	94
	25	89		9	92
	2	89		61	89
	5	88		6	86
2	27	93	9	62	97
	5	92		7	93
	3	91		61	92
	4	90		60	92
	1	89		8	92
	59	88		6	89
3	5	99	10	22	92
	27	92		15	90
	2	91		14	87
	4	89		13	86
	59	88		6	86
	1	88		2	86
4	59	97	11	23	97
	1	97		12	97
	29	90		22	85
	2	90		15	85
	5	89		10	81
	3	89		29	78
5	3	99	12	11	97
	27	93		23	94
	2	92		15	86
	4	89		22	85
	1	88		10	81
	59	87		29	78
6	61	95	13	14	99
	9	89		6	87
	62	88		10	86
	14	88		61	85
	60	87		9	85
	13	87		62	82
7	60	97	14	13	99
	8	97		6	88
	62	96		10	87
	9	93		61	85
	61	89		9	85
	6	85		62	83

OTUs	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
15	22	93	22	15	93
	10	90		10	92
	16	89		16	88
	12	86		2	88
	11	85		12	85
	2	85		11	85
16	24	89	23	11	97
	15	89		12	94
	22	88		15	84
	10	85		22	83
	2	85		29	80
	64	82		10	79
17	18	91	24	16	89
	28	80		64	85
	64	79		22	83
	67	78		29	82
	21	77		21	82
	68	76		2	82
18	17	91	25	59	90
	26	74		1	89
	28	72		4	87
	20	71		3	86
	19	71		5	85
	67	70		2	83
19	20	100	26	67	76
	28	88		17	76
	67	83		64	74
	57	83		21	74
	69	82		18	74
	68	81		69	73
20	19	100	27	5	93
	28	88		2	93
	69	83		3	92
	67	83		4	88
	57	83		1	87
	68	81		59	85
21	64	94	28	69	94
	67	82		57	94
	24	82		67	92
	28	81		68	91
	16	81		20	88
	20	80		19	88

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
29	4	90	36	63	94
	59	89		55	94
	1	89		41	94
	2	85		40	94
	27	83		34	94
	10	83		66	92
30	31	94	37	38	96
	46	84		32	96
	49	83		66	94
	54	82		63	93
	45	82		55	93
	63	81		50	93
31	30	94	38	37	96
	46	87		53	94
	54	86		45	94
	48	85		32	94
	49	84		66	93
	50	83		65	92
32	37	96	39	65	97
	38	94		44	96
	66	92		43	96
	49	92		45	95
	55	91		42	95
	50	91		63	94
33	63	93	40	34	99
	55	93		63	98
	47	93		55	98
	40	93		41	98
	34	93		66	96
	41	92		65	96
34	40	99	41	63	98
	63	98		40	98
	55	98		34	98
	41	98		66	97
	66	96		65	97
	65	96		55	97
35	45	97	42	43	98
	65	96		65	97
	63	96		44	96
	55	96		45	95
	44	96		41	95
	54	95		39	95

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
43	65	98	50	66	95
	42	98		48	94
	44	97		46	93
	45	96		41	93
	41	96		37	93
	39	96		35	93
44	65	99	51	70	92
	63	97		54	76
	55	97		36	76
	45	97		32	76
	43	97		49	75
	41	97		48	75
45	65	98	52	32	89
	63	97		66	88
	55	97		37	88
	44	97		63	87
	35	97		55	87
	43	96		50	87
46	54	96	53	38	94
	48	95		66	93
	35	94		45	93
	50	93		65	92
	37	93		44	92
	55	92		37	92
47	41	95	54	48	97
	40	95		46	96
	34	95		35	95
	66	94		63	93
	65	94		55	93
	63	94		45	93
48	54	97	55	63	100
	46	95		40	98
	35	95		34	98
	50	94		45	97
	65	93		44	97
	63	93		41	97
49	54	92	56	58	98
	48	92		63	91
	46	93		55	91
	32	92		40	91
	63	90		34	91
	55	90		46	90

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
57	69	99	64	21	94
	68	97		67	85
	67	96		24	85
	28	94		69	82
	20	83		28	82
	19	83		16	82
58	56	98	65	44	99
	63	91		45	98
	55	91		43	98
	41	90		42	97
	40	90		41	97
	34	90		39	97
59	1	99	66	41	97
	4	97		63	96
	25	90		55	96
	29	89		40	96
	3	88		34	96
	2	88		65	95
60	8	97	67	69	96
	7	97		57	96
	62	94		68	94
	9	92		28	92
	61	91		64	85
	6	87		20	83
61	6	95	68	69	97
	62	93		57	97
	9	92		67	94
	60	91		28	91
	8	89		64	81
	7	89		20	81
62	9	97	69	57	99
	7	96		68	97
	60	94		67	96
	8	94		28	94
	61	93		20	83
	6	88		64	82
63	55	100	70	51	92
	41	98		54	77
	40	98		48	77
	34	98		49	76
	45	97		50	75
	44	97		36	75

APPENDIX II. Run 2 of phenetic analysis - nearest neighbours list.

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
1	32	98	8	33	97
	31	97		7	97
	4	97		35	94
	25	90		9	92
	2	90		34	90
	5	89		6	90
2	27	92	9	35	97
	4	91		7	94
	32	90		33	93
	5	90		8	92
	3	90		34	91
	1	90		6	90
3	5	98	10	22	89
	27	92		15	89
	4	90		14	86
	2	90		6	86
	32	89		13	85
	1	89		4	85
4	32	97	11	23	96
	1	97		12	95
	31	96		22	84
	2	91		15	82
	3	90		10	79
	5	89		29	78
5	3	98	12	23	95
	27	93		11	95
	2	90		22	83
	4	89		15	81
	1	89		10	80
	32	88		29	77
6	34	95	13	14	98
	35	90		6	87
	33	90		10	85
	9	90		34	84
	8	90		9	84
	7	89		22	83
7	33	97	14	13	98
	8	97		6	88
	35	95		10	86
	9	94		34	85
	34	90		22	85
	6	89		9	84

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
15	22	89	22	15	89
	16	89		10	89
	10	89		2	86
	2	83		16	85
	14	82		14	85
	11	82		11	84
16	15	89	23	11	96
	24	87		12	95
	22	85		22	82
	10	84		15	81
	2	84		10	79
	4	82		29	78
17	18	91	24	16	87
	37	72		4	84
	36	72		22	83
	24	72		2	83
	28	71		36	82
	20	70		27	82
18	17	91	25	32	90
	24	72		1	90
	26	70		31	89
	36	68		4	88
	20	68		5	86
	37	67		3	86
19	20	99	26	36	72
	28	85		37	70
	39	82		18	70
	37	82		39	69
	30	80		28	69
	40	79		24	69
20	19	99	27	5	93
	28	85		3	92
	37	82		2	92
	39	81		4	87
	30	80		1	87
	40	79		32	86
21	36	90	28	39	94
	24	78		30	93
	37	76		40	92
	38	75		38	91
	28	75		37	91
	25	75		20	85

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
29	32	88	36	21	90
	4	88		24	82
	1	88		37	80
	31	87		39	79
	3	83		38	79
	2	83		28	78
30	39	97	37	39	95
	40	94		40	94
	38	94		38	92
	28	93		30	92
	37	92		28	91
	20	80		20	82
31	32	97	38	40	95
	1	97		39	95
	4	96		30	94
	25	89		37	92
	2	88		28	91
	29	87		36	79
32	1	98	39	30	97
	31	97		40	96
	4	97		38	95
	25	90		37	95
	2	90		28	94
	3	89		19	82
33	8	97	40	39	96
	7	97		38	95
	35	94		37	94
	9	93		30	94
	34	92		28	92
	6	90		24	79
34	6	95			
	35	92			
	33	92			
	9	91			
	8	90			
	7	90			
35	9	97			
	7	95			
	33	94			
	8	94			
	34	92			
	6	90			

APPENDIX III. Run 3 of phenetic analysis - nearest neighbours list.

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
1	2	91	8	9	93
	17	76		33	90
	20	73		29	89
	25	72		26	89
	19	72		6	89
	16	72		3	89
2	1	91	9	8	93
	17	82		6	90
	20	79		34	88
	21	78		32	88
	25	77		29	88
	19	77		26	88
3	8	89	10	14	95
	9	88		32	93
	6	86		6	93
	33	85		34	92
	29	85		26	91
	26	85		15	91
4	5	91	11	5	96
	26	90		26	95
	32	89		12	95
	29	89		32	94
	12	89		29	94
	11	89		34	93
5	26	97	12	32	97
	12	96		34	96
	11	96		26	96
	32	95		5	96
	29	95		33	95
	34	94		31	95
6	26	94	13	32	97
	15	94		34	95
	34	93		31	95
	32	93		15	95
	29	93		14	95
	10	93		12	95
7	26	94	14	32	96
	29	93		13	95
	12	93		10	95
	5	93		34	94
	11	92		12	94
	32	91		15	93

OTU	Neighbours	%ge sim.	OTU	Neighbours	%ge sim.
15	32	97	22	35	91
	34	96		25	75
	33	96		7	74
	31	95		6	74
	26	95		19	73
	13	95		8	73
16	29	93	23	29	88
	32	92		26	87
	26	92		33	86
	15	92		5	85
	6	92		34	84
	34	91		31	84
17	9	88	24	33	91
	19	87		32	88
	16	87		25	88
	20	86		20	88
	8	86		15	88
	6	86		26	87
18	34	92	25	19	94
	12	92		32	92
	33	91		26	92
	32	91		15	92
	31	91		5	92
	14	91		34	91
19	25	94	26	29	98
	20	92		5	97
	32	91		12	96
	21	91		34	95
	26	90		32	95
	15	90		15	95
20	19	92	27	28	96
	25	89		33	87
	24	88		26	86
	29	87		16	85
	26	87		12	85
	21	87		5	85
21	33	91	28	27	96
	19	91		26	85
	12	90		12	85
	34	89		5	85
	32	89		33	84
	29	89		32	84

OTU	Neighbours	%ge sim.
29	26	98
	31	96
	34	95
	12	95
	5	95
	32	94
30	32	96
	34	95
	12	95
	31	94
	15	94
	26	93
31	34	96
	32	96
	29	96
	15	95
	13	95
	12	95
32	34	97
	15	97
	13	97
	12	97
	31	96
	30	96
33	15	96
	12	95
	34	94
	32	94
	26	94
	5	94
34	32	97
	31	96
	15	96
	12	96
	30	95
	29	95
35	22	91
	25	76
	19	74
	7	74
	6	74
	29	73

A note on Claparède organs in larvae of the superfamily Eupodoidea (Acari: Acariformes)

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Claparède organs occur in the larvae of acarine taxa which possess genital papillae in nymphal and adult stages. Although the presence of these organs in the Eupodoidea has been remarked upon previously by several authors, there have been no detailed descriptions or figures given. In this study, the occurrence of Claparède organs is confirmed in five genera of Eupodoidea, two for the first time. Scanning electron microscopy revealed details of their external morphology.

Introduction

The name 'Claparède organ', first proposed by Grandjean (1940), acknowledges the first worker to observe these acarine structures (Claparède 1868). They have also been referred to by a number of other names, for example, urstigma, bruststiele and larval organs.

Claparède organs are confined to prelarval and larval mites and then only to those taxa where genital papillae appear in subsequent stages. They are thus present in all Oribatida and many members of the Actinedida and Acaridida. Exceptions may be found in the prelarvae and larvae of certain species of Halacaridae (Krantz 1977) and Bdelloidea (Grandjean 1938, 1946), which lack Claparède organs even though the nymphal and adult stages possess genital papillae.

Claparède organs are located between coxae I and II. Usually, only one pair occurs; but multiple organs, and also multiple genital papillae in the corresponding postlarval stages, are present in some freshwater Hydrachnellae and Halacaridae (Grandjean 1948, Bartsch 1973). They vary in form between taxa (Grandjean 1938, 1946, 1955, Knülle 1959, Bartsch 1973, Lions 1973, Coineau 1974, Vercammen-Grandjean 1975, Krantz 1977, Alberti 1979), but always resemble their respective genital papillae in external appearance (Grandjean 1938, 1946, Knülle 1959, Krantz 1977).

The similarities between Claparède organs and genital papillae led to speculation of a common function for the two structures. Grandjean (1946, 1955) and Vercammen-Grandjean (1975) respectively suggested they were humidity receptors and respiratory organs. Detailed studies using staining techniques (Bartsch 1973) and electron microscopy (Alberti 1979), however, have provided evidence for both playing an osmoregulatory role. Alberti also noted the similarity, in both structure and attributed function, between Claparède organs and genital papillae and the coxal vesicles of certain lower insects, such as the Diplura.

In the Eupodoidea, the first pair of genital papillae appears in the protonymph, with a second and final pair being added at the deutonymphal stage. This being the case, it is to be expected that eupodoid prelarvae and larvae would possess Claparède organs. In several descriptions of larval eupodoids there are no references to their presence (Willmann 1936 a, 1936 b, Pittard 1971, Gless 1972). Other authors, however, did observe them in the prelarva of species of *Linopodes* and *Rhagidia* (Ehrnsberger 1974) and of *Eupodes strandtmanni* (Coineau 1976), in the larvae of the genera *Eupodes*, *Penthaleus* and *Rhagidia* (Grandjean 1945, 1946, Ehrnsberger 1974) and in the families Eupodidae and Rhagidiidae (Knülle 1959). None of these works includes descriptions or figures of the Claparède organs. This study, consequently, aims to establish the presence or absence of Claparède organs in larval eupodoid mites and, where present, to record details of their external morphology.

Materials and methods

Larvae of the genera *Cocceupodes*, *Eupodes*, *Halotydeus*, *Penthaleus* and *Rhagidia*, for examination under the optical microscope, were obtained from a collection of mites mounted and cleared in 70% lactic acid.

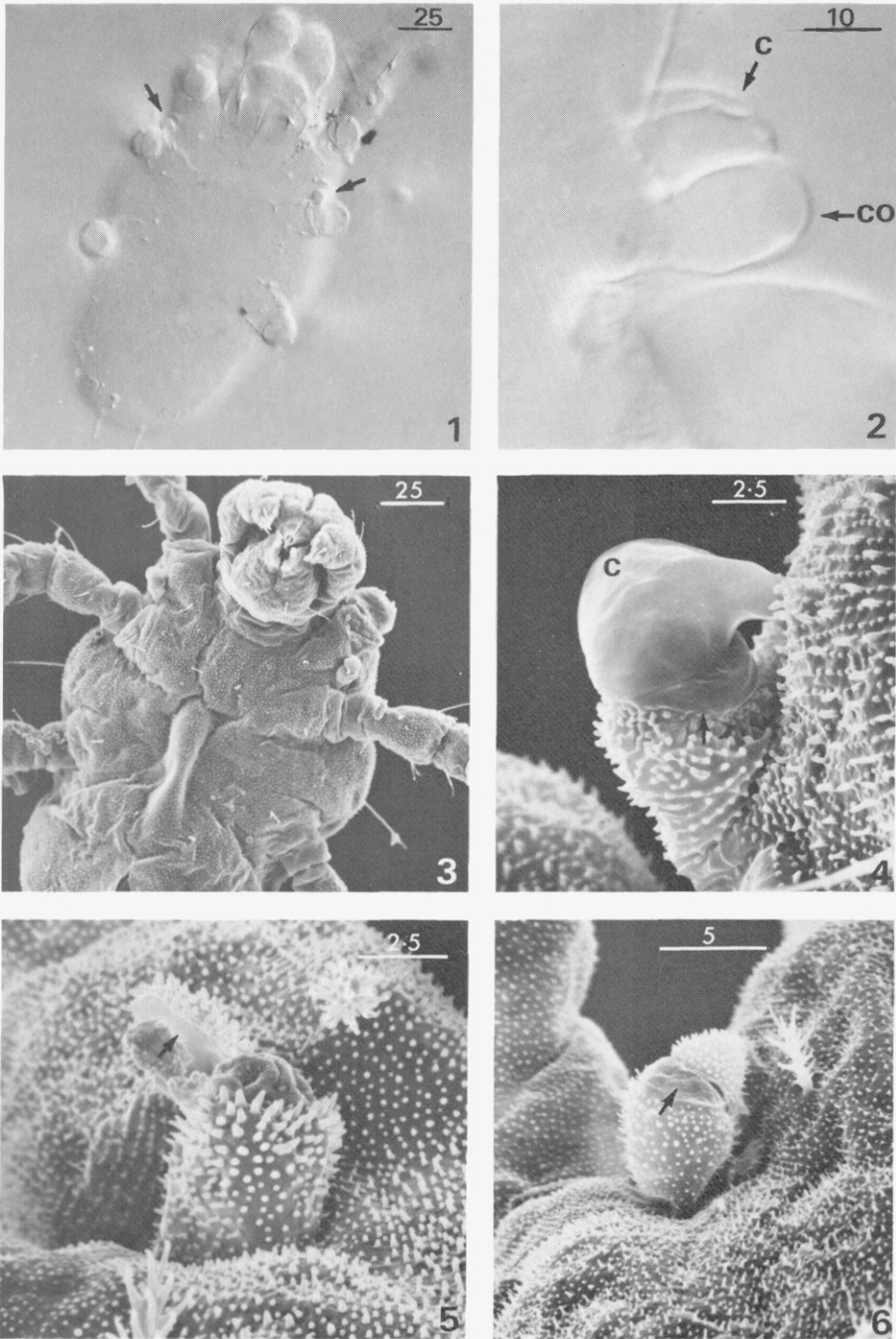
Fresh specimens of *Cocceupodes trisetatus* Strandtmann and Prasse, *Cocceupodes* sp. 1 and 2 and *Penthaleus* sp., for scanning electron microscopy, were extracted from soil samples by means of controlled-gradient Berlese funnels into 70% methylated ethyl alcohol. They were then rinsed in distilled water and freeze-dried. The dried specimens were mounted on aluminium scanning electron microscope stubs and sputter-coated with a 15 nm thick layer of a gold-palladium mixture.

Results and discussion

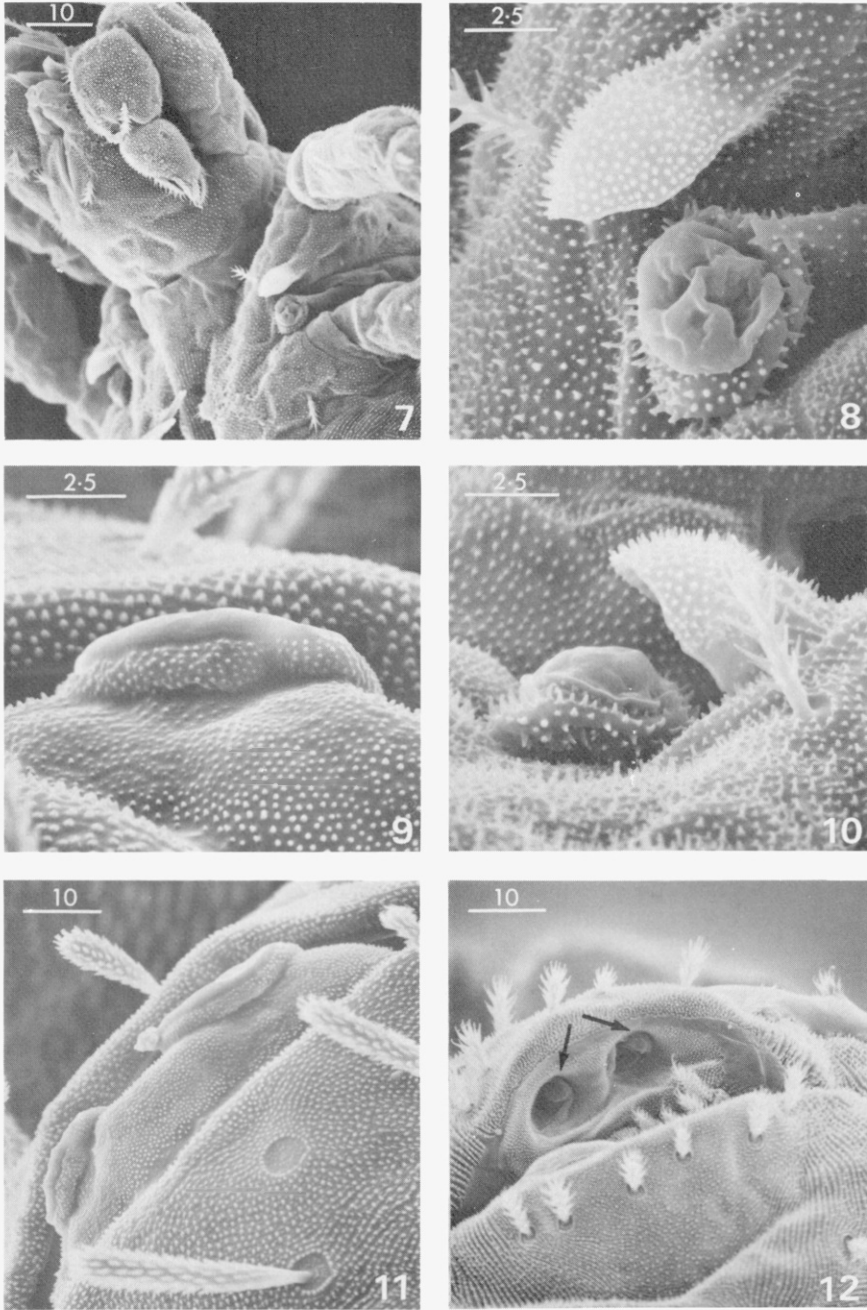
The examination of mounted larvae confirms that Claparède organs occur in species of the genera *Eupodes* (arrows, fig. 1), *Penthaleus* and *Rhagidia* and establish for the first time their presence in the genera *Cocceupodes* and *Halotydeus* (fig. 2). Although minute morphological details are difficult to discern, it is possible to see that the organ has the same general form in all taxa, consisting of a cylindrical protuberance, rounded distally, with an associated 'cap'.

Scanning electron micrographs (figs 3–12) of the Claparède organs clearly show that the protuberance arises laterally between coxae I and II (figs 3 and 7). It possesses a spiculed integument like that covering the coxae, while the apical dome is smooth (figs 5, 6, 8 and 10). As in other superfamilies, eupodoid Claparède organs resemble the genital papillae of the nymphs and adults (fig. 9). The cap originates from the base of the posterior free margin of coxa I (fig. 7). Its shape and position is such that it can cover the smooth dome (arrow, figs 4 and 6). According to Alberti (1979), this ability prevents water-loss. The under-surface of the cap is smooth (arrow, fig. 5) while, in larvae of examined species of *Cocceupodes*, the upper-surface has a coxal-type integument (figs. 5, 6 and 8); in *Penthaleus* sp., by contrast, both surfaces are smooth (fig. 4). Another difference in the form of the cap can be seen at its attachment point. In species of *Cocceupodes* it is broadly based (figs 8 and 10), whereas in *Penthaleus* sp. it is stalk-like (fig. 4).

Although usually stored beneath the genital flaps (arrows, fig. 12), the genital papillae are sometimes extruded (fig. 11), for example, during oviposition or, in terrestrial species, for the uptake of water (Alberti 1979). Extrusion is effected by hydrostatic pressure, while the papillae are retracted by the contraction of muscles attached to their base (Prasse 1970). There is some evidence that Claparède organs have



FIGS. 1-6. Claparède organs. (1) *Eupodes* sp., ventral view, Claparède organs arrowed; (2) *Halotydeus* sp., Claparède organ with associated cap; (3) *Penthaleus* sp., ventral view, (4) *Penthaleus* sp., smooth dome of Claparède organ, arrowed, covered by cap; (5) *Cocceupodes* sp. 1, Claparède organ, smooth under-surface arrowed; (6) *Cocceupodes trisetatus*, smooth dome of Claparède organ, arrowed, partially covered by cap. Measurements on scale bars in μm . Abbreviations, co = Claparède organ, c = cap.



FIGS. 7–12. Claparède organs and genital papillae. (7) *Cocceupodes* sp. 2, ventro-lateral view showing location of Claparède organ and cap; (8) *Cocceupodes* sp. 2, Claparède organ withdrawn; (9) *Eupodes* sp., genital papilla everted; (10) *Cocceupodes* sp. 2, lateral aspect of withdrawn Claparède organ; (11) *Eupodes* sp., genital papillae extruded between genital flaps; (12) *Cocceupodes* sp., genital papillae, arrowed, retracted. Measurements on scale bars in μm .

a similar facility for movement as, in several specimens, they appear to be somewhat withdrawn (figs. 8 and 10).

Due to the scarcity of larval eupodoids in collections, it has not been possible to determine the presence or variation of Claparède organs throughout the superfamily. However, as they are now known to occur in five genera, and all are of the same basic form, it seems likely that similar organs will be found in most, if not all, genera of the Eupodoidea.

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