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PAUROPODA - THE SMALLEST MYRIAPODS

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The Study of Pauropoda, the smallest of the "myriapods" began some 125 years ago with Sir John Lubbock's paper "On Pauropus, a New Type of Centipede" (Lubbock, 1866). He regarded it as neither a chilopod nor a diplopod although he described it as "at first sight looks like a Chilopod; indeed the compactness of the body, the dorsal plates and the elongation of the posterior legs give it much resemblance to a small Lithobius".

Pauropus huxleyi, at 1/20 of an inch (1.2mm) he termed "a bustling, active, neat and cleanly little creature". "It has, too, a look of cheerful intelligence, which forms a great contrast to the dull stupidity of the Diplopods, or the melancholy ferocity of most Chilopods". He also described a second species Pauropus (now Stylopaauropus) pedunculatus. The drawings on p.13 are from his original paper.

In the early part of the twentieth century R.S.Bagnall published a series of papers which included references to and descriptions of species of Pauropoda (see in: Scheller, 1990) but it seems that some of his descriptions were inadequate for accurate diagnosis of his species. A list of his species occurs in Blower (1987) but Scheller (loc.cit.) has provided a revised list. Various papers by Remy (1956, 1961) included British species, Turk (1967) produced lists for British caves, Scheller (1974) dealt with pauropods from arable soil, Moore (1982) species from a coal shale heap and Oliver and Amsden (1982) gave an account in "Nature in Wales" which included scanning electron micrographs.

In 1990 Ulf Scheller produced his up to date list (Scheller, 1990) in which he listed 23 species, four new to Great Britain and one new to science. It was that paper which prompted the present account in the hope that other workers might become interested in the group.

DESCRIPTION OF PAUROPODA

A valuable description of the characteristics of pauropods and of the features useful in diagnosis of genera and species is
DESCRIPTION OF THE PLATE.

PLATE X.

Fig. 1. *Pauropus Huxleyi*. Seen from above, × 70.
Fig. 2. " " Seen from below, × 70.
Fig. 3. " " Outline of head, × 125.
Fig. 4. " " Mouth-parts, × 250.
Fig. 5. " " Hair on head, × 250.
Fig. 6. " " Antenna, × 250.
Fig. 8. " " Base of appendage.
Fig. 9. " " Portions of appendage.
Fig. 10. " " Anterior leg, × 250.
Fig. 11. " " Second leg, × 250.
Fig. 12. " " Posterior leg, × 125.
Fig. 13. " " Appendage on underside of posterior leg.
Fig. 14. " " Appendage on underside of antepultimate leg.
Fig. 15. " " Appendage at the base of second pair of legs, × 250.
Fig. 16. " " Spermatozoa.
Fig. 17. " " Posterior segment seen from above, × 250.
Fig. 18. " " Young.
Fig. 19. " " Base of second pair of legs, × 125.
Fig. 20. *P. pedunculatus*. Termination of antenna, × 250.

Fig. 1 PAUROPIDAE : Lubbock’s original drawings
Fig. 2 PAUROPIDAE, based on Scheller (1988)
a. Hypothetical male (Pauropodidae), lateral
b. "    "    "    dorsal
c. Hypothetical head, antennae not shown,
   setae rows indicated, F1-F3 flagellae
d. Hypothetical antenna (Allopauroopus type)
   setae labelled
e. Hypothetical leg
f. Hypothetical pygidium, sternal view
   setae labelled
given by Scheller (1988) from which much of the present account is derived. Throughout the world some 570 species in 30 genera have been recorded: of these 502 species in 15 genera are in the family Pauropodidae, nearly two thirds in the genus Allopauroopus (Scheller & Østerdahl, 1989).

Pauropoda are described as progoneate, dignathous, blind animals with biramous antennae, generally 0.5 to 1.5 mm long and with nine to eleven leg bearing segments in the adult. Body shape is variable; British forms are either elongate, whitish animals such as Pauropus which are widely distributed or are almost discoidal with heavily sclerotised tegites as in the recently discovered Trachypauroopus britannicus Scheller, 1990, at present our only representative of the Eurypauropodidae. The description here relates to the widespread former type.

The body is cylindrical with 9-10 pairs of legs in the adult; most species are more or less long legged and they are often speedy runners for short distances. Identification is based on external structure especially the characters of the head setae, the antennae, the tergites and their projections, legs and their characteristics, and the pygidium.

Head: tergal side triangular, with many setae, a single one between the bases of the antennal ramus and then four transverse rows. On either side of the head is a prominent ovoid temporal organ, a large, cornea-like disc covering a fluid filled chamber containing sensory receptors.

Antennae: biramous, the two branches protruding from a four segmented stalk. One branch (the tergal) has one flagellum, the other (sternal) has two together with one or two globuli and one or two setae. Globuli are club shaped sensory organs seen between the two flagellae. The last segment of the stalk also bears setae. The shape, length and thickness of these structures are used in separating genera and species.

Trunk: twelve segments, the first (the collum) has vestiges of a pair of legs on its much expanded ventral side. Legs are lacking on the last two segments (last segment only in Allopauroopus subgenus Decapauroopus). Tergites are thin or very slightly sclerotised; the shape of the tergites, their division into sclerites and the number, arrangement and shape of spines, setae and other protuberances are used taxonomically. There are five pairs of long trichobothria on tergites II-VI.

Legs: five or six segmented; the number of segments, the shape of the tarsus and the setae on that and on the coxa and trochanter are used taxonomically.

Pygidium: horizontally divided, the tergum with 4-5 pairs of setae, the sternum with one to three pairs of setae and an anal plate projecting from its posteromedian part. This latter, rather peculiar structure, is a small sclerotised plate often
with branches and/or appendages of various sizes and shapes. This structure, even in the immature stages, constitutes a unique system of characters that often helps to immediately identify a species. The pygidial setae are also valuable in identification.

BIOLOGY

Pauropods occur in strata from litter to subsoil and are found in samples along with other litter organisms but, because of their small size, are often missed. They seem to occur in most soil types but rarely in heavy, peaty or very wet soils. They also occur in litter, decaying logs, under bark and in moss carpets where conditions are suitable. Not being able to burrow, pore space is of prime importance but they are very sensitive to humidity, temperature and light levels and also to insecticides.

In most environments occurrence is very patchy and populations sparse but locally up to several hundred specimens per square metre have been found in deciduous forests. Starling (1944, quoted in Wallwork, 1970) quotes densities over one million per acre (250 per sq. m.) in oak and pine stands in eastern North America.

LIFE CYCLE

Tiegs (1947) describes the life cycle of Pauropodidae and illustrates the egg to fourth larval stadia whilst Lawrence (1953) illustrates egg and early larval stadia.

The eggs, which are spherical, whitish and about 0.05-0.15 mm in diameter are laid singly or in clumps in the soil. After about two weeks the outer membrane breaks and a quiescent pupoid (pilarva) phase occurs. This lasts for a few days (3-4 is quoted by Wallwork) and may have outgrowths showing the position of antennae and more or less the first three pairs of legs. The pupoid gives rise to a hexapod first stadium with seven abdominal segments which in turn gives a second stadium with five pairs of legs after about three weeks. The third and fourth larval instars have six and eight pairs of legs respectively. The adults have eight, nine or ten pairs of legs and occur about three to four months from egg laying.

COLLECTION OF PAUROPODS

Many workers have not seen pauropods except by accident in collections of other material and their small size makes collection difficult. Following Ulf Scheller's paper at the Manchester Congress there was some discussion regarding these animals, partly about finding them (Scheller, 1974):
"The best method to spot them on the underside of a stone is to blow gently over the surface. They can be recognised immediately by the manner in which they run. Although superficially like the slow moving collemboians, pauropods (the common Pauropodidae) run rapidly forwards, they stop, they run backwards or twist their bodies in many directions". In his 1988 report he refers to them as showing "mouse like movements".

Other than hand collection, pauropods can be found in numbers by flotation methods, including simple water flotation. Most funnels will produce results but Tullgren funnels are best for collectig agile forms. Eurypauropodidae are most conveniently obtained by Winkler funnels. Pauropods are very susceptible to slightly too high or too low moisture levels, light, etc. and it is important that the laboratory atmosphere is not too dry, forcing them inwards, not downwards in funnels.

EXAMINATION OF SPECIMENS

Because proper orientation of the animals and extension of the pygidium greatly facilitates work, animals should be fixed and preserved in fluids which keep them soft, transparent and stretched. Cold strong alcohol gives irregular contraction so strength should not exceed 70% and the drawbacks of alcohol are often eliminated if it is mixed with small amounts of acetic acid and formaldehyde.

Examination must be carried out with a high power microscope (dissecting microscopes are not adequate) and the specimen should be placed on a microscope slide. Large specimens, especially heavily sclerotised ones have to be cleared e.g in lactic acid. Using a coverslip with a thin cork wedge (15mm x 1.5mm at its thickest end) allows movement of the animal and examination without damage by moving the wedge. Most specimens will require 1000x magnification; the use of phase contrast facilitates the examination of many structures.

Once identified the specimens may be rinsed and stored in alcohol in small upright glass vials. Specimens may be mounted (e.g in Hoyer's fluid) but these are of limited value to the taxonomist.

IDENTIFICATION

Identification is based on various characters as indicated. There are no reliable keys at present and there are also taxonomic problems with some species because of the nature of early descriptions. If possible, all identifications should be checked by a specialist familiar with the group.
As indicated above, identification of these animals is something of a specialist activity. A key to families is given by Schubart (1964) but this is no longer of great value in the light of present understanding of the systematics of the group.

The present keys are devised by Dr. Scheller:

**KEY TO HIGHER TAXA**

1a. Antennal base four segmented with two antennal branches on segment 4........Order TETRAMEROCERATA...........................2

1b. Antennal base six segmented with two antennal branches, one on segment 5 of the base, the other on segment 6........Order HEXAMEROCERATA (Tropical)

2a. First and last tergites large, covering at least head and anterior part of pygidium respectively...............................Family EURYPAUROPODIDAE (One British genus, *Trachypauropus*)

2b. First and last tergites small, leaving head and pygidium free.

3a. Body generally oval, flattened; tergites most often divided and slightly sclerotised.................................Family BRACHYPAUROPODIDAE (May occur in the British Isles)

3b. Body generally fusiform; tergites most often undivided and not sclerotised; setae on tergites generally not modified........4

4a. Apical organ of tarsi globular with no distinct claws........Family AFRAUROPODIDAE (Tropical)

4b. Apical organ of tarsi with claws.................................Family PAUROPODIDAE (5 British genera)

**KEY TO BRITISH SUBFAMILIES OF PAUROPODIDAE**

1a. Sternal antennal branch with 2 setae and 2 globuli, the latter joined to a single stalk........POLYPAUROPODINAE (*Polypauropus*)

1b. Sternal antennal branch with one seta and one globulus........2

2a. Tergites thin........................................PAUROPODINAE (Allopauropus, *Pauropus*, Stylopaupropus)

2b. Tergites more or less sclerotised......SCLEROPAUROPODINAE (Scleropaupropus)
KEY TO BRITISH GENERA IN PAUROPODINAE

1a. Stalk of antennal globulus distinctly longer than diameter of globulus. ...................................................... Stylopauporus

1b. Stalk of anterior globulus shorter than diameter of globulus. ................................................................. 2

2a. Anterior and posterior margins of sternal antennal branch of equal length .................................................. Pauropus

2b. Anterior margin of sternal antennal branch shorter than posterior margin ................................................. Allopauporus s.l. Allopauporus

3a. Adults with 9 pairs of legs, seta b3 of pygidial sternum present .............................................................. Allopauporus s.g. Allopauporus

3b. Adults with 9 or 10 pairs of legs, seta b3 of pygidial sternum absent .......................................................... Allopauporus s.g. Decapauporus

(BRACHYPAUROPODIDAE: Bagnall (1911) described a species, Brachypauporus lubbocki from London but this is a nomen dubium (Scheller, pers comm.; also in Scheller, 1990)).

EURYPAUROPODIDAE: One species, Trachypauporus britanicus Scheller 1990 described from mixed deciduous forest, Waterbarrow, west bank of Lake Windermere (coll. J.G. Blower, Tullgren extraction).

SCLEROPAUROPODINAE: One species, Scleropauporus lyrifer is recorded by Scheller (1990) from Wye College Farm, Kent (coll. R.C. Clutterbuck, 1972). Bagnall (1935) described S. hansenii from the London area but this is another nomen dubium.

(ASPAERIDOPIDAE: A. ashworthi Bagnall, 1935, Scotland: This family has been suppressed; larval stages of Pauropodidae (Scheller, 1970))

POLYPAUROPODINAE: One species, Polypauporus duboscqui is recorded from Berkshire (Scheller, 1974).

PAUROPODINAE: See key to genera above.

CHECK LIST OF BRITISH SPECIES
(After Scheller, 1990)

County and, where known, Vice-county are given

Family PAUROPODIDAE
Subfamily PAUROPODINAE
Genus Allopauropus sg. Allopauropus s.str.
A. brevisetus Silvestri: Avon(6), Northumberland(67) doubtful
A. danicus (Hansen): Avon(6), Herts(20), Lancs(59), Durham(66), Lothian

Genus Allopauropus sg. Decapauropus
A. broelemanni Remy: Somerset(5), Strathclyde(?99)
A. cuenoti (Remy): Somerset(5), Kent(15), London, Glos(33), Humberside
Durham(66), Northumberland, Strathclyde(?99)
A. distinctus Remy: Cumbria(69), Mid Glamorgan(41)
A. gracilis (Hansen): Dorset(9), Somerset(5, 6), Hants(12), Surrey(17)
Berks(22), London, Glos(33), Essex, Leics(55),
Lincoln(53), Lancs(69), N. Yorks, Durham(66),
Northumberland, S. Glamorgan(41), Lothian(82), Strathclyde (99), Co. Kerry (Ireland)

A. helveticus (Hansen): Somerset(6)
A. milloti Remy: Glos(33)
A. millotianus Leclerc: Somerset(5)
A. multiplex Remy: Berks(22), Surrey(17), Kent(15), Glamorgan(41)
A. productus Silvestri: Lothian (doubtful)
A. remyi (Bagnall): Lothian
A. thalassophilus Remy: Lothian
A. vulgaris (Hansen): Somerset(5), Wilts(8), Kent(15), Lancs(69),
Durham(66), Northumberland(67), Mid Glamorgan (41), Co. Kerry (Ireland)

Genus Pauropus
P. fuscifer Silvestri: Oxon(23), Durham(66), Lancs(?69)
P. huxleyi Lubbock: London
P. lanceolatus Remy: Somerset(8), Wilts(7), Lancs(59)

Genus Stylopauropus
S. brito Remy: Devon(3), Surrey(17)
S. pubescens (Hansen): Northumberland

Subfamily SCLEROPAUROPODINAE

Genus Scleropauropus
S. lyrifer Remy: Kent(15)

Subfamily POLYPAUROPODINAE

Genus Polypauropus
P. duboscqui Remy: Berks(22)

Family EURYPAUROPODIDAE
Subfamily EURYPAUROPODINAE

Genus Trachyopauropus
T. britannicus Scheller: Lancs(69)
REFERENCES


