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MILLIPEDES

Keys and notes for the identification of the species

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Foreword

Millipedes, along with the earthworms and centipedes, live in the soil and leaf-litter; all three were probably grouped together and called 'creepy-crawlies' when we first met them as children. Gardeners, horticulturalists and foresters will be quite familiar with them, with their characteristic hard bodies and numerous legs. Like earthworms, millipedes have an effect upon the structure of the soil and are important agents in the breakdown of leaf-litter, fallen branches and old tree-stumps in woodlands.

This *Synopsis* should enable the present millipede fauna of the British Isles to be accurately identified. This is important as this fauna is ever-changing due to the introduction of animals in the soil of imported plants. These introductions may enrich the British fauna but may also be to its detriment, when the introduced species extend their range at the expense of the indigenous fauna. The work of the British Myriapod Survey begun in 1971 is therefore to be both applauded and encouraged. *Millipedes* should assist considerably by providing a well-illustrated aid to the identification of the diplopodan or millipede section of the Survey.

Millipedes can be regarded as the second edition of *British Millipedes (Diplopoda) No. 11* in the original series of *Synopses* published in 1958. The new much-enlarged work is by the same author, Gordon Blower; it reflects his personal contribution to the study of millipedes in the intervening years, also his expertise as an artist and collector. Most of the illustrations have been made from specimens which the author has collected himself; these he has dissected and displayed so as to demonstrate taxonomic characters with clarity.

The publication of this *Synopsis* may have been delayed because of the author's desire to make the book as complete as possible; it sets a high standard of description and illustration which the Editors have encouraged and appreciated. To Mr Blower, they say simply and most sincerely 'Thank you' and this will be echoed by all those who have an interest in the soil of our land, be it for work or pleasure, and probably most of all by those undertaking the British Myriapod Survey.

R. S. K. Barnes
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Introduction

There are four classes of arthropods loosely grouped together as the Myriapoda; these are the Diplopoda (millipedes), Chilopoda (centipedes) and the lesser known Pauropoda and Symphyla, for which we do not have common English names. The features shared by these four groups are the head with a single pair of antennae, mandibles and one or two pairs of maxillae, and many (more than four) *similar* leg-bearing segments. The Crustacea have many appendages but these are not all similar and are often biramous. Myriapod legs are uniramous and this feature they share with insects. The various pterygote and apterygote groups of hexapods and the four groups of myriapod have recently been considered to be independently evolved classes of the UNIRAMIA deriving from a lobopod ancestor with some of the characters of the present day *Peripatus* (Manton, 1977).

The essential point is that millipedes are as distinct from centipedes, for example, as they are from any group of insects. The structure of the millipede **head**, with short elbowed **antennae** probing the substrate, robust **mandibles** of a very peculiar type, and just one pair of **maxillae** fused into a characteristic lower lip or **gnathochilarium**, is quite unlike that of a centipede with long filiform antennae, rather small mandibles, *two* pairs of maxillae and robust poison claws operating horizontally under the head. So obvious are the adaptations of a centipede for offence and carnivory and the contrasted adaptations of the millipede for defence and saprophagy that it seems almost unnecessary to restate the fact that millipedes have two pairs of **legs** on each segment in contrast to centipedes which have only one pair on each segment. Millipedes are almost unique among the Uniramia in possessing only two pairs of jaws (mandibles and maxillae); their *dignathous* condition is only shared by the little known group of Pauropoda.

The Class Diplopoda is the largest of the four myriapodan classes. In the *Synopsis of British Millipedes* (Blower, 1958), I gave Dr. Schubart's estimate of 8,000 described species, only 44 of which were then known to occur in Britain. During the twenty-seven years which have elapsed since the publication of the 1958 edition eight more species have been added to the British fauna and another, previously allowed only varietal status has now been elevated to specific rank. However, the number of described species in the world has risen to 10,000. Hoffman (1979) has recently suggested that an additional 70,000 species may remain undiscovered or undescribed.

Our 52 species seems a poor share of the European fauna when compared with 250 species in France (Demange, 1981) and 160 in Germany (Schubart, 1934), but compares favourably with 45 species in Holland (Jeekel, 1978) and 39 in Denmark (Enghoff, 1974). These latter countries have the advantage of mainland connections but are smaller in area. However, the British species belong to six different orders and give a fair representation of the adaptive radiation within the class. Furthermore, our few species occur in fertile grassland and forest soils at densities of one to four hundred individuals per square metre and may comprise a half to two-thirds of the biomass of arthropods.

Whilst only a few species have been added during the last twenty years or so, the details of the life-histories of most of our common species have been unravelled during this period and it is now possible to identify every one of the eight to fourteen juvenile stadia of some dozen species. This degree of precision is of course necessary if a quantitative estimate of the role of millipedes in soil ecosystems is to be obtained. Writing at the end of the last century, one of our most distinguished zoologists working with millipedes said that British millipedes should soon be as well known as the British butterflies (Pocock, 1893). At this time there were sixteen species on the British list. In the first half of this century substantial progress towards the goal mentioned by Pocock was made, especially by Bagnall and Brade-Birks. The bibliographical check list of Brade-Birks (1939) listed 41 species and provided the foundation of our modern knowledge. However, by 1970, although one and a quarter thousand vice-county records from 250 published papers and many unpublished sources had been accumulated, eighteen counties were without a single record and three quarters of the counties had less than half the possible number of species recorded in them (Blower, 1972, 1974b). In 1971 the British Myriapod Survey was set up and in its first five years 359 further vice-county records were made (Fairhurst *et al.*, 1978) and in the next five years, up to 1980, 547 more records had been added (Fairhurst, pers. com.). In the first ten years the Survey has increased the number of English and Welsh records by 50% but has more than doubled the number in Scotland and Ireland. At this rate of progress the British millipedes should indeed become as well known as the British butterflies within the next decade. This *Synopsis* is designed to facilitate the rapid and accurate recording of the details of the distribution and abundance of these animals.

General organization

In a diplopod there is a **head** followed by a **trunk** consisting of a number of **leg-bearing** segments or **rings**, one or more **apodous rings** and finally a tail-piece or **telson** (Fig. 1). Most of the trunk units or rings carry **two pairs of legs**; they are therefore double segments or **diplosegments**. The first four rings may represent single segments and hence we use the non-committal term 'ring' to denote the trunk unit whether double or single.

The head or head capsule

The head capsule carries the **antennae**, the **eyes** (ocelli) and in some orders, **the organs of Tömösvary** (see Figs. 16, 25). Laterally the 'cheeks' or coxomeres of the **mandible** articulate with the cephalic capsule. Ventrally is the lower lip or **gnathochilarium**. The short antenna is composed of eight joints or **antennomeres**; the diameter of the fifth and sixth antennomeres is greater and gives the antenna a clubbed appearance; a right-angled bend in the region of antennomeres 3 and 4, whilst 5 carries the apex of the antenna ventralwards to enable the terminal **sense organs** to palpate the substrate immediately in front of the head. Behind the antennal base may be located a group of ocelli. These are absent in all species of the order Polydesmida, in some blaniulids and, in Britain, two species of julid. In 1978 Paulus stated that the visual units of myriapods are not homologous with insect ocelli but represent disintegrated facetted eyes (quoted by Haupt, 1979).

There are only two pairs of **jaws** or mouthparts. The **mandible** (Fig. 2) is robust and is remarkable amongst the uniramians possessing three separate **coxomeres**: the **cardo**, the **stipes** and the **gnathal lobe.** The **cardines** (sing. cardo) and **stipetes** (sing. stipes) are visible laterally and form the sides of the head (the 'cheeks'). In the Chordeumatida a small groove on the edge of the cheek adjacent to the head capsule is the only evidence of the division between cardo and stipes. These imperfectly separated basal lobes of the mandibles are voluminous and project as a pair of jowls, laterally beyond the edges of the dorsal head capsule (Figs. 22, 25). In the other orders the cardo is completely divided from the stipes and they do not project much beyond the lateral limits of the head capsule. The gnathal lobes of the mandibles are articulated mesially and are therefore not visible laterally; they are visible from in front (Figs. 53A and B) where they can be seen performing their characteristic rolling movements. Ventrally, the gnathal lobes of the mandibles are hidden by the gnathochilarium which is formed from the **first maxillae**. The detailed shape of this lower lip varies from order to order

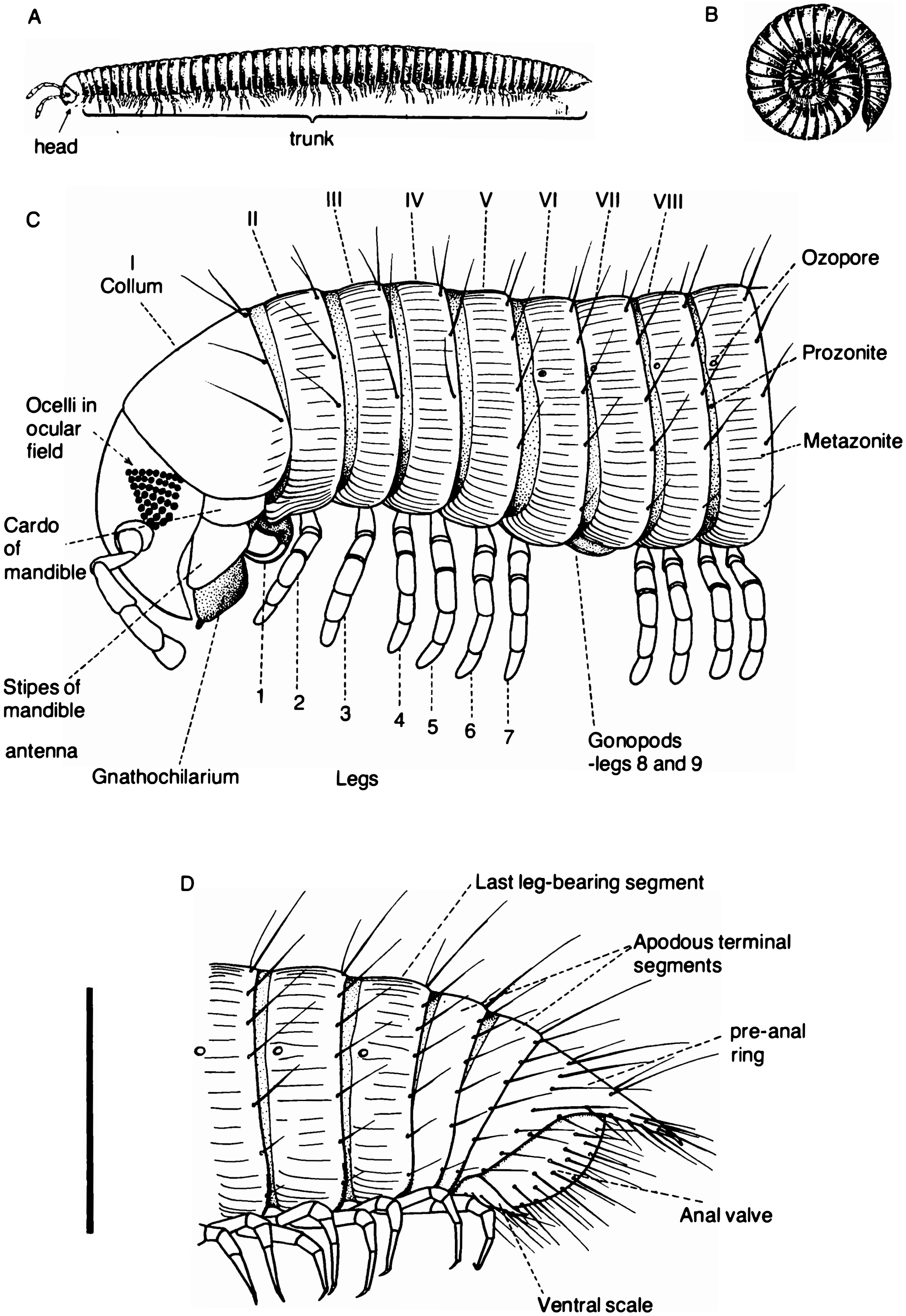

Fig. 1. A. *Julus scandinavius*, female walking normally, drawn from a photograph by S. M. Manton; B. The same female as A in protective spiral position; C. The head and the first rings of a stadium X mature male *Ophyiulus pilosus*: The anterior

but essentially it forms the floor of the buccal cavity and carries lobed sense organs along its anterior edge.

The structure of the trunk units: tergites, pleurotergites and rings

A typical arthropod **segment** has two principal **sclerites**, a dorsal **tergite** and a ventral **sternite**; in addition, there is usually some sclerotisation of the lateral area or pleuron to form **pleurites**. Such a simple arrangement is found in the bristly millipedes of the order POLYXENIDA, but here most of the segments are double and one diplotergite covers a pair of diplopleurites and two single sternites, one for each segment. The POLYXENIDA are separated from all other diplopods into the subclass PENICILLATA. The other two subclasses, PENTAZONIA and HELMINTHOMORPHA are characterized by the impregnation of the sclerite cuticle by calcium salts.

In the pill millipedes of the order GLOMERIDA the diplosegment is covered by a strongly arched diplotergite which extends laterally, displacing the diplopleurites to a ventral position; mesial to the diplopleurites are two sternites, one in front of the other (Fig. 3B). The name of the subclass, PENTAZONIA refers to these five freely articulated sclerites which make up the trunk unit (Fig. 3).

The remaining orders have more diplosegments than the bristly millipedes and the pills and are placed in the subclass HELMINTHOMORPHA. In the order POLYZONIIDA the diplosegments are **pentazonian** (Fig. 3C), but in all other millipedes (the majority of species) the diplopleurites are fused to the arched diplotergites to form the **pleuro-tergal** arch. In the order CHORDEUMATIDA (Figs. 3D, E and F) the two sternites of the diplosegment are freely articulated by arthrodial membranes within the ventral space of the pleuro-tergal arch; this is the **trizonian** condition, referring to the three sclerites, pleurotergite and two sternites, which form the trunk unit. In the orders JULIDA and POLYDESMIDA the sternites are usually fused to the pleurotergal arch and to each other to form a completely cylindrical sclerite; this is the **monozonian** condition (Figs. 3A, G, H, and I). In British species of the Nemasomatidae, the sternites are not fused to the arch but are tightly articulated with it; they are not freely movable within the gape of the pleurotergite as they are in the Chordeumatida.

Unlike the **collum**, or first trunk unit, all the rest are narrower in front than behind (Figs. 1 and 2). An anterior **prozonite** is distinguished from a posterior **metazonite**. The prozonite of one unit is overlapped by the metazonite of the preceding unit. The two zones are separated by a distinct suture in the Julida where the unit is almost perfectly cylindrical (Figs. 1,

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legs appear to emerge from the ring in front of that to which they belong; D. The tail end of the same male as C showing the last three podous rings, two apodous rings terminated by the telson consisting of the pre-anal ring, anal valves and ventral scale.

3A). In the Polydesmida (Figs. 3G–I) the metazonite of the pleurotergite is produced laterally or dorso-laterally into lobes or keels, the **paranota**, which give the unit a trapezoidal or quadrangular section and the appearance of a flat or arched back. In the CHORDEUMATIDA one family, the Chordeumatidae (Fig. 3D), have smoothly cylindrical pleuro-tergites like the Julida and two others (Craspedosomatidae, Brachychaeteumatidae) (Figs. 3E, F) have pleurotergites produced into paranota. The occurrence of flat-backed and arched-backed species in both Chordeumatida and Polydesmida and of cylindrical species in both Chordeumatida and Julida is the main cause of faulty ordinal diagnosis by the beginner.

Trunk units of individuals of the Polyxenida, Glomerida and Polyzoniida are properly specified as tergites, those of the Chordeumatida as pleurotergites, and those of the Polydesmida and Julida simply as **rings**, but in accounts which follow the term **ring** is frequently used regardless of the order. In the orders with complete rings the sternites of the first and second pairs of legs are not fused to the pleurotergal arch but are freely articulated with it. In the Julida the first three trunk units are incomplete ventrally (Fig. 5). In the Polydesmida the ventral edges of the pleurites of the second and third units are connected by narrow sclerotised bridges thus leaving only the first ring incomplete ventrally (Figs. 61L, 67D).

The sequence of the trunk units

The first unit is the **collum** (Figs. 1 and 2). It is covered dorsally by a tergite; its sternite is not in evidence ventrally but is attached to the base of the gnathochilarium as the **hypostoma** or **gula** (Fig. 2). In the Julida the collum tergite overlaps the head in front and the second ring behind. In British Chordeumatida and Polydesmida the collum tergite is smaller and there is less overlap (Figs. 20–22, 25, 62, 64, 67, 70–73). In the Glomerida (Figs. 15–17) the tergite of the second trunk unit is much larger than those following and extends further laterally. In the polydesmidan *Prosopodesmus* (Fig. 60A) the paranota of the second ring extend further laterally than those of all subsequent rings. With these exceptions, the units following the collum are all built upon the same plan. However, the collum and the following three trunk units share three pairs of legs between them and it is not immediately evident to which of the four units the three pairs of legs belong. The collum and the next three units may be single segments or they may be double having lost one or both of their two pairs of legs. For descriptive purposes it will be assumed that the collum is apodous and that leg-pairs 1, 2 and 3 belong to trunk units II, III and IV. The podous part of the trunk will be regarded as consisting of a series of podous units, including the probably single units I, II, III and IV and the fact that one of these units appears to be apodous will be disregarded.

A pair of **ozadenes** or stink glands open by **ozopores** mid-laterally on the sixth to the last podous rings of the snake millipedes (order Julida); their

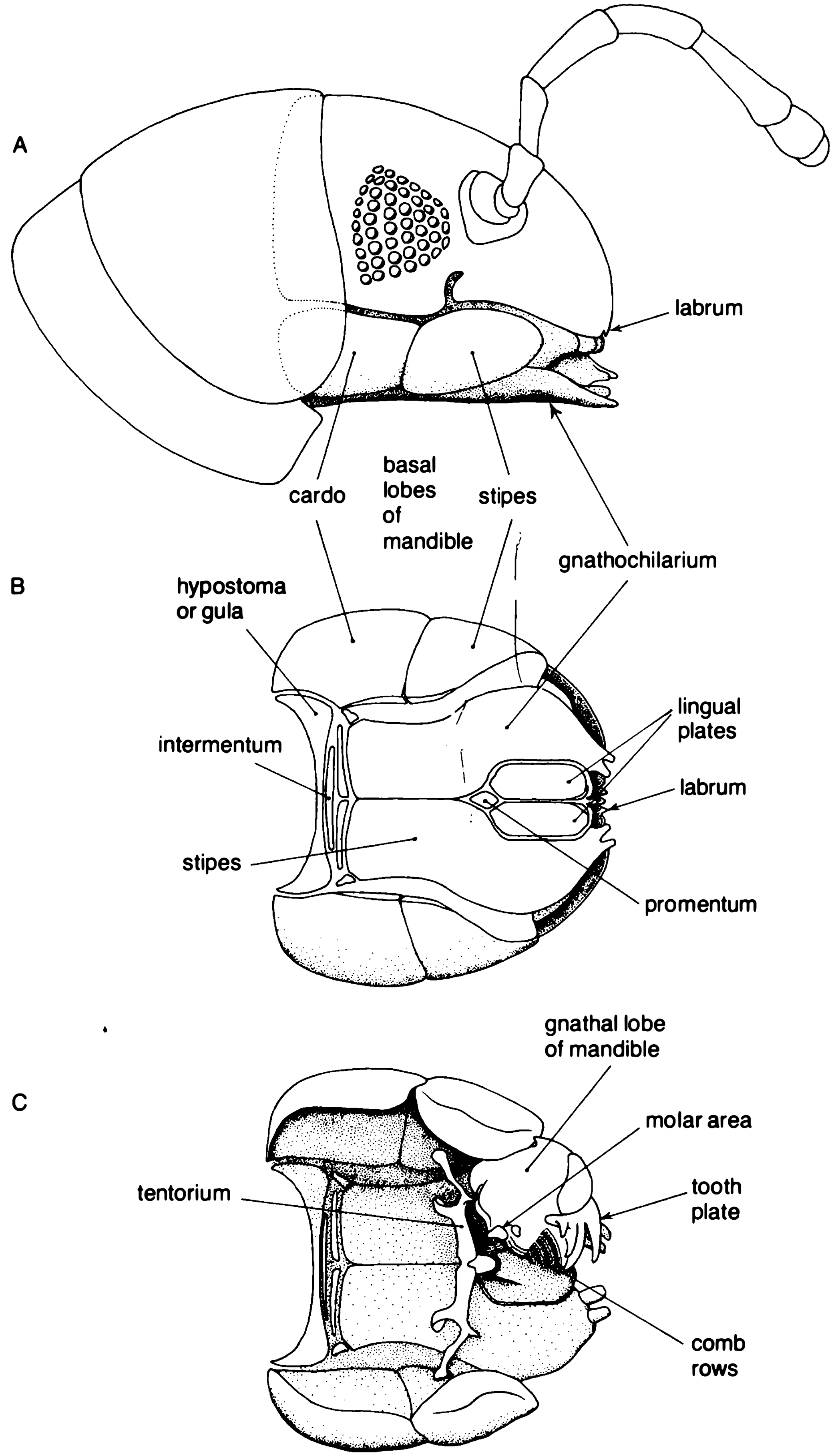

Fig. 2. The mouth parts of a julid millipede, *Julus scandinavius*: A. Anterior of body in lateral view; B. Ventral view of head to show gnathochilarium; C. Dorsal view after removal of the dorsal part of the head capsule and clearing away the soft parts.

coloured contents are often an obvious feature (Fig. 33D, E). In the flat- or arched-backed millipedes of the order Polydesmida the ozadenes are not so obvious; they open on the lateral edges of paranota V, VII, IX, X, XII, XIII and XV–XIX (Figs. 70 and 71), except in *Prosopodesmus* where they open on postero-lateral tubercles of all the diplopodous rings (Fig. 60). In pill millipedes, paired ozadenes open by a single mid-dorsal ozopore. British species of the order Chordeumatida are without these organs of defence.

Following the podous series of trunk units there are one or more apodous units; the rudiments of the ozadenes may be apparent on each of them. In the monozonian orders (and, with certain qualifications, the Chordeumatida) the apodous units of one **stadium** develop legs and are added to the podous series of the next (see post-embryonic development p. 17). Terminating the trunk is the telson. This consists of a **pre-anal ring** often produced postero-medially as a caudal projection or 'tail', a pair of ventro-posterior **anal valves** which move apart like a pair of doors during defaecation from the anus and a ventral **sub-anal scale** (Fig. 1D). Between the apodous rings and these structures lies the proliferation zone where new trunk units are initiated and develop. Thus the so-called pre-anal and anal 'segments' are clearly post segmental and form the terminal telson.

Legs

Millipede **legs** articulate with the sternites in contrast to centipede legs, for example, which originate from the pleura. The ventral origin in millipedes is seen by Manton (1958) as an adaptation to burrowing by minimizing the lateral projection of the legs. In the Polydesmida where the extended paranota provide some protection, the legs have a more lateral origin due to the sternites becoming transversely extended (compare Fig. 4, A, B and C).

Just slightly anterior and lateral to the coxae are the openings of the tracheal system, the **spiracles**; there is a pair of spiracles on each sternite, two pairs on each diplosternite. Due to the more lateral placement of the coxae in the Polydesmida the spiracles are visible in a lateral view, see for example Figs. 62 and 67. The spiracles open into a spacious atrium or **tracheal pouch** from which arise numerous unbranched **tracheae**; the tracheal pouch serves as an apodeme for the attachment of the extrinsic muscles of the coxae.

As Manton (1958) has pointed out, the ventral insertion of the legs necessitates an acute S-shaped flexure, down from the **coxa**, up and round to the 'knee' via the **trochanter, prefemur** and **femur**, and then down again through the **postfemur, tibia** and **tarsus** to make contact with the ground by the **tarsal claw** (Fig. 4). To permit this S-shaped bending, millipede legs have one extra podomere compared with the legs of arthropods with legs arising more laterally. The postfemur might be regarded as this extra podomere; its position usually corresponds with the 'knee' and is analagous in position to the spider patella. The millipede leg then has a basic number of seven **podomeres** in

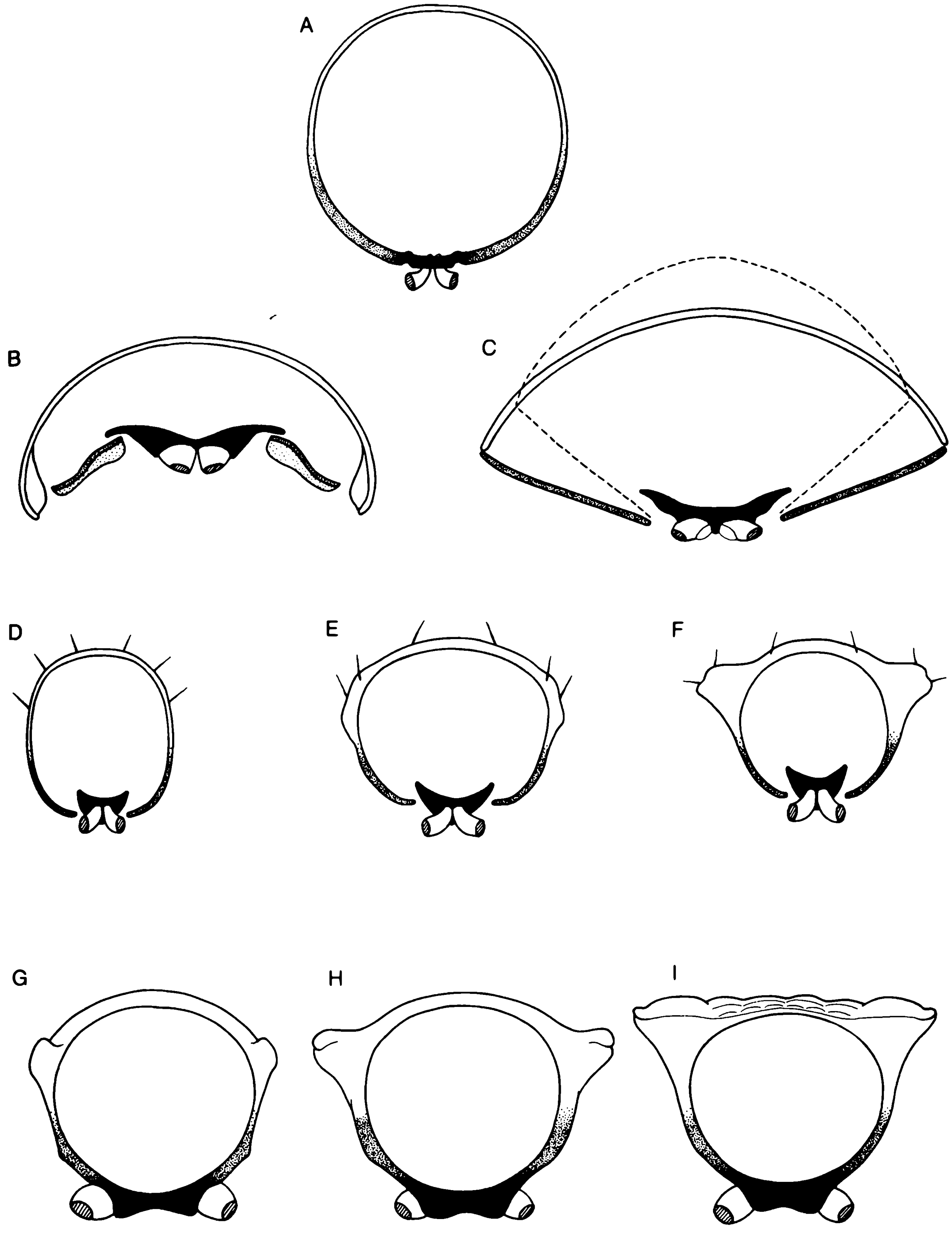

Fig. 3. Transverse sections showing the ring architecture of diplopods: A. MONOZONIA, Julida: tergite, pleurites and sternites united into a complete ring; B, C. PENTAZONIA, with separate tergite, pleurites and sternites; B. Glomerida, *Glomeris marginata;* C. Polyzoniida, *Polyzonium germanicum*; D, E, F. TRIZONIA, with tergite and pleurites fused into a pleurotergal arch, but sternites free. D. *Melogona*; E. *Craspedosoma*; F. *Nanogona* (paranotal expansions in E and F). G, H, I. MONOZONIA, with paranotal expansions: Polydesmida. G. *Stosatea*, H. *Oxidus*, I. *Polydesmus*. Sternites black, pleurites stippled, tergites plain.

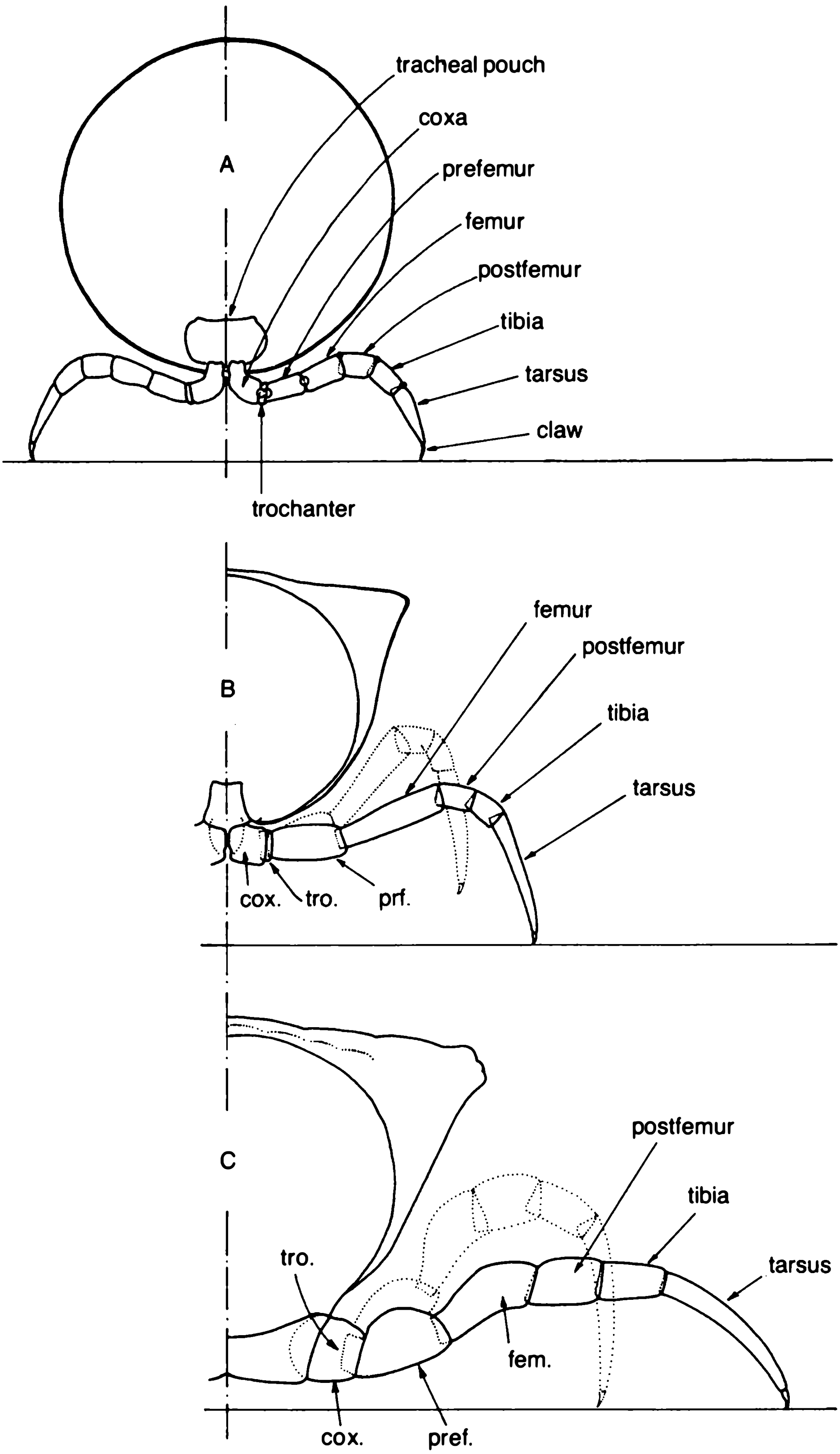

Fig. 4. Millipede legs. Drawings of the normal stance of A, a julidan; B, a chordeumatidan, *Nanogona polydesmoides* female; C, a polydesmidan, *Polydesmus angustus*, male. The legs are shown in posterior view. The three figures are drawn to an approximately common diplosegment volume so that leg lengths are directly comparable.

contrast to the chilopods with six and most insects with five (disregarding the multiarticulated tarsus).

However, the second podomere or trochanter is rather short and may be fused with the coxa (e.g. in Glomerida) or so far recessed into the coxa that it is only visible on the side of the leg opposite the flexion and is easily overlooked. Millipede legs are unguligrade (to borrow a term from vertebrate anatomy), applying just the tip of the leg, the tarsal claw, to the ground. Most insects are plantigrade, applying the whole tarsus, sometimes several jointed, to the ground. Only in *Polyxenus* is there a divided tarsus, and in some exotic millipedes. The tarsal claw (which is not usually counted as a distinct podomere, although it has all the hallmarks of one) is often provided with an accessory claw (not actually claw-like); this is usually well-developed and often longer than the claw itself in Chordeumatida and Julida but is absent from Polydesmida.

In the most forceful burrowers, the Polydesmida, the individual podomeres are short and stout (Fig. 4C); at the opposite extreme, the legs of the Chordeumatida, which are designed for fleetness rather than force, the podomeres are long and thin (Fig. 4B). Animals in the order Chordeumatida, with or without paranota, have legs which are more slender overall and longer in relation to the diameter of the trunk, than the legs, for example, of the Julida (compare Fig. 4, A and B).

Mention is made in the next section of various modifications of certain legs in the male millipede. In these secondary sexual structures, the basal coxa is often the most profoundly modified and it is useful to distinguish this from the remaining podomeres which are collectively named the **telopodite.** (Note that the term *telopod* is applied to the terminal legs of a male pill millipede and has a different meaning.)

The secondary sexual characters

All diplopods are progoneate; the genital ducts of both sexes open on ring III; in males of Julida and Polyzoniida the paired deferent canals open into a median **penis** or **penes** behind the second pair of legs (Fig. 5); in Glomerida, Chordeumatida and Polydesmida the male openings perforate the coxae of the second pair of legs. In females of all orders each oviduct opens separately into an organ called the **vulva** behind the second pair of legs (Fig. 5). Each

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In A, the circles between coxa and trochanter, trochanter and prefemur, and prefemur and femur indicate the positions of bicondylar pivot joints which allow both flexion and extension; the black dots placed dorsally between the more distal podomeres (femur and postfemur, and through to the claw) indicate dorsal hinge joints which allow flexion only. The same distribution of pivots and hinges applies also to drawings B and C. Note in C, the trochanter is entirely within the coxa; the semi-annulus between coxa and prefemur is arthrodial membrane.

The positions of the legs shown by dotted lines in B and C are those adopted when pushing upwards with their flat backs. Redrawn and simplified from Manton, 1958.

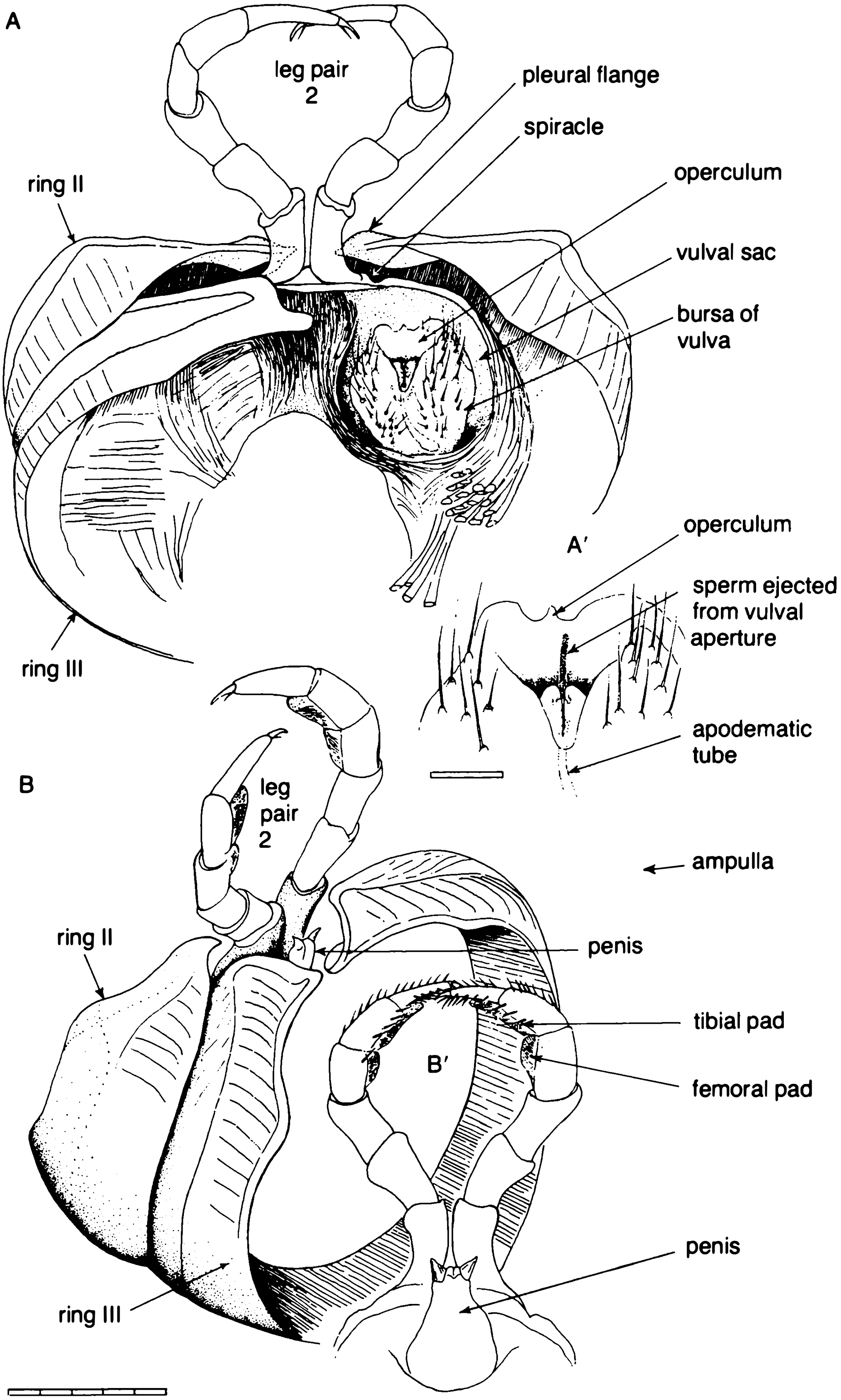

Fig. 5. The genital openings of a julid *Tachypodoiulus niger*: A. Ring II and the right side of ring III of a female with the second pair of legs and the vulvae behind; ventro-posterior view. On the animal's left the pleurite of ring III has been removed and the vulval sac trimmed to reveal the vulva within; A′. Enlarged view of the apex of the isolated left vulva from behind. (Note that in A it is clearly not possible to detach the second pair of legs anteriorly and keep the vulvae attached unless the

vulva consists of a body or bursa rather like the hinged shells of a bivalve mollusc with the gape directed anteriorly and covered by an **operculum** (Figs. 5, 48–50). Within the body of the vulva is an **apodematic tube** ending in one or two **ampullae** which serve as seminal receptacles or **spermathecae.** Each vulva lies in a **sac** sunk into the lumen of the ring behind the second pair of legs; the sac and its vulva are everted during copulation. The **epigynal region** (the anterior ventral edge of the third ring) and the vulvae are sometimes useful for identification.

In the Penicillata there are no other obvious secondary sexual modifications. In the Glomerida (pill millipedes) the last three pairs of legs in the male are modified as **gonopods**; the last pair are gonopods proper, the **telopods** (Fig. 15C); adult males of the Helminthomorpha (all diplopods except Glomerida and *Polyxenus*) one or both of the pairs of limbs on the seventh ring (limb pairs 8 and 9) are modified to form the apparatus by means of which sperm is introduced into the female (in the colobognath *Polyzonium* limb pairs 9 and 10 are modified into gonopods). In millipedes where both 8th and 9th pairs are transformed, one of the two pairs act as the actual intromittent organs, the gonopods proper and the other pair serve as gonopod protectors (**peltogonopods**) or some other accessory function. In the Chordeumatida, Craspedosomatidea, the modified 8th limbs form the gonopods proper and the 9th form the paragonopods (Figs. 20–22); in the Chordeumatida, Chordeumatidea (Figs. 26, 27) and in the Julida (Fig. 13), the 9th pair form the gonopods proper and the 8th pair serve as peltogonopods. In the Polydesmida only the 8th pair of limbs are modified as gonopods, the 9th remain as normal walking legs (Figs. 61F, 67A).

In the Chordeumatidea, in addition to the modifications of ring VII, the posterior pair of legs of ring VI are modified as anterior **paragonopods** and also both pairs of limbs on ring VIII are modified, the 10th pair are rudimentary and the 11th pair form the posterior paragonopods (Figs. 28, 29). In all the Helminthomorpha the form of the gonopodial apparatus is absolutely specific and is often the only reliable means of identification.

In the Julida there are additional secondary sexual modifications in the male; the cheek lobes (cardo and stipes) may be produced ventrally (Fig. 12B), the gnathochilarium may be inflated (Fig. 1C), the first pair of legs are often profoundly modified into a pair of hook-like structures (Fig. 12B) and the coxae of the second pair of legs are sometimes produced and carry glands (Fig. 53). In the Polydesmidae all the legs of the male are noticeably stouter than those of the female. In Julida, the legs of the male may carry special adhesive pads to help him keep a secure hold on the female (Fig. 5B, B′). Further details are given in the sections on each order.

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flanges on ring II are removed). B. Ring III and right hand side of ring II of the male, with the second pair of legs and the bilobed penis behind, vento-posterior view from a little to the right side; B′. Posterior view of the isolated second pair of legs with penis behind. (Note in B and B′ the sole pads on the tibia and postfemur.)

Internal anatomy

The **alimentary system** consists of (1) an ectodermal (cuticle lined) fore-gut or **oesophagus**, (2) an endodermal mid-gut or **mesenteron**, usually the longest part and the site of digestion and absorption and (3) an ectodermal **hind-gut** (Fig. 6A and C). In most millipedes the gut runs a straight course from mouth to anus but in the short-bodied Glomerida the hind gut loops forwards and back again. An anterior **salivary gland** opens into the roof of the **pre-oral cavity** and a **posterior gland** lies along the fore-gut and opens on the gnathochilarium. **Anal glands** open into the final eversible part of the hind gut and contribute to the building of moulting chambers and nests.

There are two organs of excretion. A pair of **maxillary glands**, each of which consists of a **sacculus** in the head opening into a long tube, the **labyrinth**, which passes posteriorly and then loops back, coiling around the descending branch, to open on the gnathochilarium. There is a single pair of **Malpighian tubules** arising from the junction of mid and hind gut, passing forwards to the head end and returning back along the whole length of the trunk and ending blindly (Fig. 6).

The **gonads** lie between the gut and the ventral **nerve cord** and open on ring III, on or just behind the second pair of legs (Fig. 6B). The **ovaries** are paired, but in all except Chordeumatida, they are housed in a common median **ovitube** which bifurcates anteriorly into short **oviducts** opening into the **vulvae** behind the second pair of legs (Fig. 6D, E). In julids the paired ovaries within the ovitube run from about ring XV to the last podous ring. In a ripe female the eggs are packed tightly within the tube which occupies about half the ring volume. Eggs found anterior to ring XV usually form a single row and are passing forwards for laying.

In most orders there is a single pair of tubular **testes** running the length of the trunk in a position analagous to the ovitube; each opens separately on the coxae of the second pair of legs, or through a bilobed **penis** just behind the legs. Transverse connectives run between the two testes like the rungs of a ladder. In Glomerida, there is a single median testis tube with a row of pouch-like follicles either side; this tube bifurcates anteriorly into a pair of vasa deferentia which open on the coxae of the second pair of legs.

Reproduction

Sperm transfer

The **sperm** received by a female is stored in blind-ending sacs (the spermathecae or seminal receptacles), in the vulvae. The initial transfer of sperm to the female is here called insemination, as distinct from the actual process of fertilization which occurs when the sperm meets the eggs as they leave the body at oviposition.

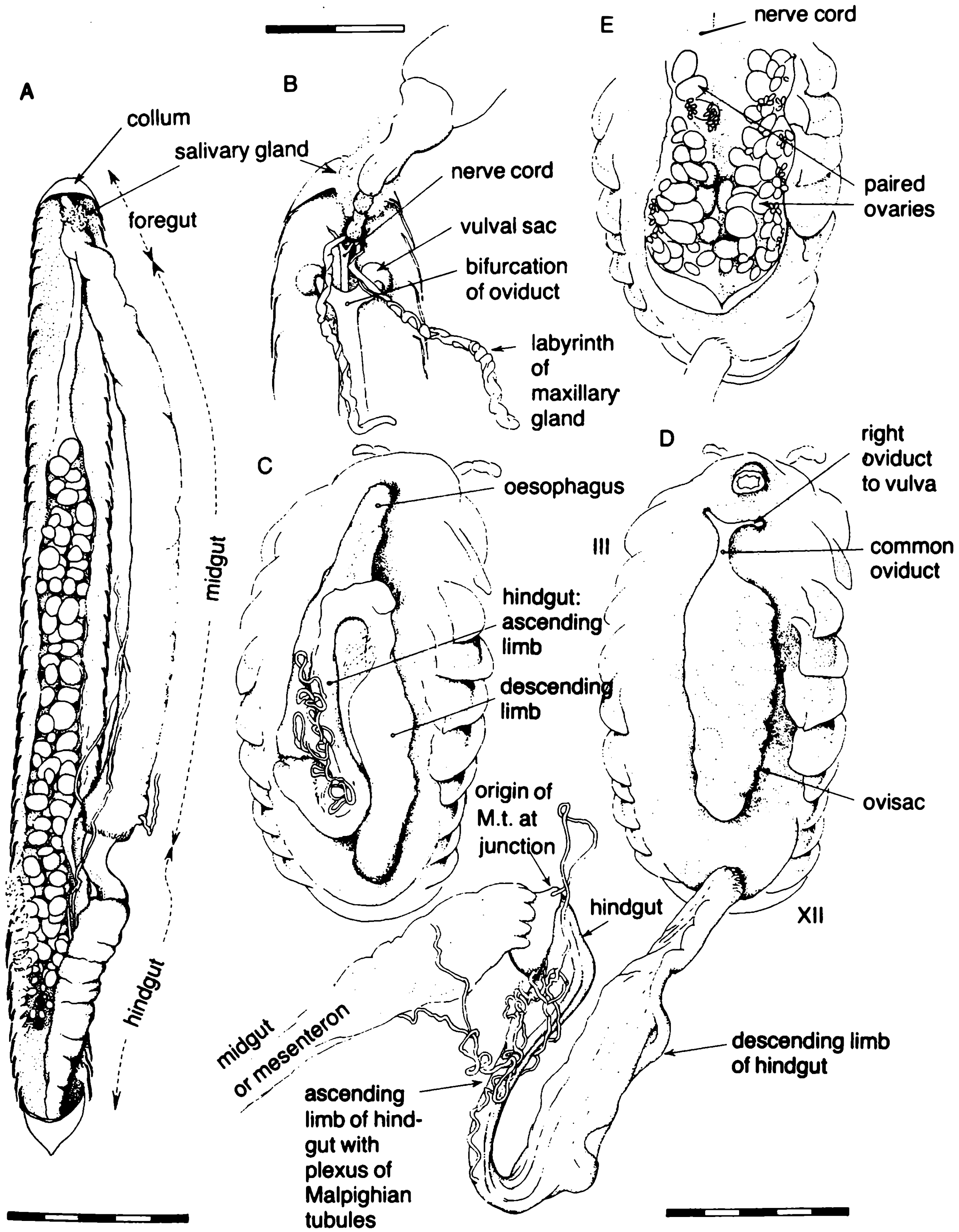

Fig. 6. Dissections of a snake and a pill millipede. *Julus scandinavius*, adult female; A. View after removal of the dorsal halves of the rings and deflection of the gut over to the right, to reveal the eggs in the ovitube. There are 73 eggs in view; a further 'layer' of 55 lies beneath – a total of 128 medium to nearly full-sized eggs. B. Enlarged view of the anterior part after folding the foregut forwards and further dissection to reveal the bifurcation of the common oviduct to supply the paired vulvae within their sacs. *Glomeris marginata*, adult female: C. View of the gut *in situ* immediately after removal of the dorsal parts of the tergites; D. The gut has been severed just behind the mouth and reflected back to reveal the ventrally placed ovisac and oviducts; E. The ovisac has been opened by a median longitudinal incision and the flaps pulled apart to reveal the paired ovaries.

Polyxenida
In the bristly millipede, *Polyxenus lagurus* (p. 53), insemination of the female is by **indirect sperm transfer**. The male deposits a **spermatophore** on to a specially constructed **silken web**. The female subsequently finds the spermatophore and takes it up into her **genital opening.** The sperm web includes special **signal threads** which guide the female to the spermatophore.

In all other millipedes there is **direct sperm transfer**. The male places the sperm directly into the female opening. However, the transfer is hardly as direct as the process known in mammals and most insects. The transfer is usually made by special **intromittent organs** called the **gonopods**, located some distance from the penes.

Pentazonia
In the pill millipedes the last three pairs of limbs in the male (limbs 17, 18 and 19) are modified; the last pair are the largest and most modified; they are usually refered to as the **telopods** (see Fig. 15C). Their role in sperm transfer is described on p. 58.

Helminthomorpha
In all millipedes except bristly millipedes and pill millipedes, the gonopods are formed from one or both pairs of legs on ring VII and serve as intromittent organs. The act of insemination must be preceded by the passage of sperm or spermatophore from the male openings on ring III, to the gonopods on ring VII. This recalls the process in spiders where the intromittent organs, the palps, are some distance from the genital openings. In chordeumatids transfer is even more complicated; the spermatophores are first transferred to the **coxal sacs** of the posterior paragonopods and from there they are passed to the gonopods proper.

Pairing

The method of bringing the gonopods opposite to the female openings varies. In most millipedes the male approaches the female, mounts upon her back from behind and follows a spiral course forwards until the ventral surfaces of both are contiguous and ring VII of the male lies opposite ring III of the female. This complicated manoevre sometimes occurs very rapidly and is difficult to follow in detail. The ventral sides of male and female are brought together in a different way in the julines *Ophyiulus pilosus* (p. 172) and *Julus scandinavius* (p. 168). Male and female approach each other head on, meet and raise their anterior ends, climbing up each other's ventral surface, so-to-speak.

Various devices facilitate pairing and ensure stability during insemination. The much stouter legs of the males of polydesmids are clearly adaptive in this respect; a pair of *Polydesmus* spp. are the most difficult to separate. The modified first pair of legs of julids appear to locate on the head capsule of the female. The median coxal processes of the leg pair 2 of male *Julus scandinavius* (p. 168) may sometimes suffer the fate of being bitten off by the female.

Parthenogenesis

A number of British millipedes can reproduce in the absence of males. Males of *Stygioglomeris crinata* (p. 60), for example, have never been found, and parthenogenesis in this species is presumed to occur. Parthenogenesis has been established in the bristly millipede, *Polyxenus lagurus* (p. 53), in the nemasomatid, *Nemasoma varicorne* (p. 102) and in the blaniulid *Proteroiulus fuscus* (p. 107), but in all these three species males are known to occur. In *Nemasoma varicorne* and *Polyxenus lagurus* there are distinct sexual and parthenogenetic forms. Males of *N. varicorne* do occur in small numbers in Britain but Dr. Enghoff has examined both sexes from this country and has found them to belong to the parthenogenetic form. British individuals of *Polyxenus lagurus* have rarely been sexed, but it is now known that the sexual form, at least, does occur here (p. 54). The subject is reviewed by Enghoff (1978b).

Oviposition

Polydesmid, julid and blaniulid females build elaborate **nests** using a pabulum of earthy faecal material cemented in position by the trowel-like action of the everted rectum. The nest of polydesmids is the most elabȯrate. Several species of these families build nests easily in captivity when kept in plastic boxes with a suitable substrate of soil. The nests are usually built against the bottom of the box and can be seen through the transparent plastic. Polydesmids in particular can be persuaded to build on the underside of a stone or piece of wood placed on the soil. Chordeumatida once called nematophorans or 'thread-carriers', construct their nests of silk. Most common species of polydesmid, julid and blaniulid lay their full complement of eggs in one nest. Other species lay a few eggs at a time and loosely coat them with earth or rectal secretion (e.g. *Proteroiulus fuscus* (p. 107) and *Cylindroiulus latestriatus* (p. 155)). Nemasomatids lay just one egg at a time. The pill millipede, *Glomeris marginata* (p. 58) coats each egg in a capsule of earthlike material; the coated egg could easily be mistaken for a faecal pellet.

Life history

Post-embryonic development

Millipede eggs are unable to hibernate or aestivate and begin to develop as soon as they are laid, in winter, spring or summer (p. 28). The egg hatches into an immobile final **embryonic stadium** called the **pupoid** (Fig. 7); this moults to give the hexapod **first post-embryonic stadium** or **instar** (Fig. 7).

This first **post-embryonic stadium**, or instar, has four fully developed rings with three pairs of legs between them.* Behind these podous rings are one, two or three apodous rings followed by the telson. These apodous rings become podous at the next moult. Further leg-bearing segments are added at ensuing moults. This mode of embryonic development is termed **anamorphosis** and is to be contrasted with the post-embryonic development of most insects which hatch from the egg with their full complement of segments; this latter type of development is called **epimorphosis**.

In the Glomerida (pill millipedes) anamorphosis proceeds up to stadium VI (*Glomeris* (p. 60)) or VII (*Stygioglomeris* (p. 62)) in which stadia the full complement of rings and legs are present (12 rings, 17 or 19 pairs of legs) but animals in these stadia have not attained maturity. Further moults follow *without* addition of new segments and legs. This mixture of anamorphic and epimorphic development (**hemianamorphosis**) also occurs in Polyxenida and in the tropical juliforms, Spirobolida and Spirostreptida.

In most millipedes development is purely anamorphic. The hexapod first stadium usually undergoes seven or eight moults to give eight or nine stadia but there may be from six to fourteen or even fifteen stadia. In the Polydesmida there are either seven or eight stadia; in the Chordeumatida there are eight or nine. The number of stadia in the Julida is more variable; there are from six to fourteen or fifteen stadia (Figs. 8 and 9).

In the Polydesmida and the Chordeumatida the increment of new diplosegments at a given moult is always the same, one, two or three in the former; one, two, three or four in the latter (see Table 1). The stadium of any individual belonging to these orders can be determined merely by counting the rings (see Table 1). In the Julida increments of new rings vary from one to eight and the increment is not always the same for a given stadium; thus the stadium cannot be determined by counting the number of rings. For example, the first stadium of *Cylindroiulus punctatus* with four podous rings may add:

either ... $2 + 5 + 5 + 5 + 6 + 5$ to give a stadium VII with 32 podous rings
or ... $2 + 5 + 7 + 7 + 7$ to give a stadium VI with 32 podous rings

Thus a given number of rings may be the result of either a smaller number of larger increments or a larger number of smaller increments.

In the Julida which possess eyes, the ocular field grows regularly at each moult; new ocelli are added in a definite sequence and the stadium can be determined by examining their number and arrangement. The first stadium is usually blind, the second stadium has one single ocellus; this is followed in the third stadium by a row of two ocelli in front of the single ocellus of the second stadium; a further row of three ocelli is added in the fourth,

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* Stadium I of *Polyzonium germanicum* is exceptional in possessing four pairs of legs.

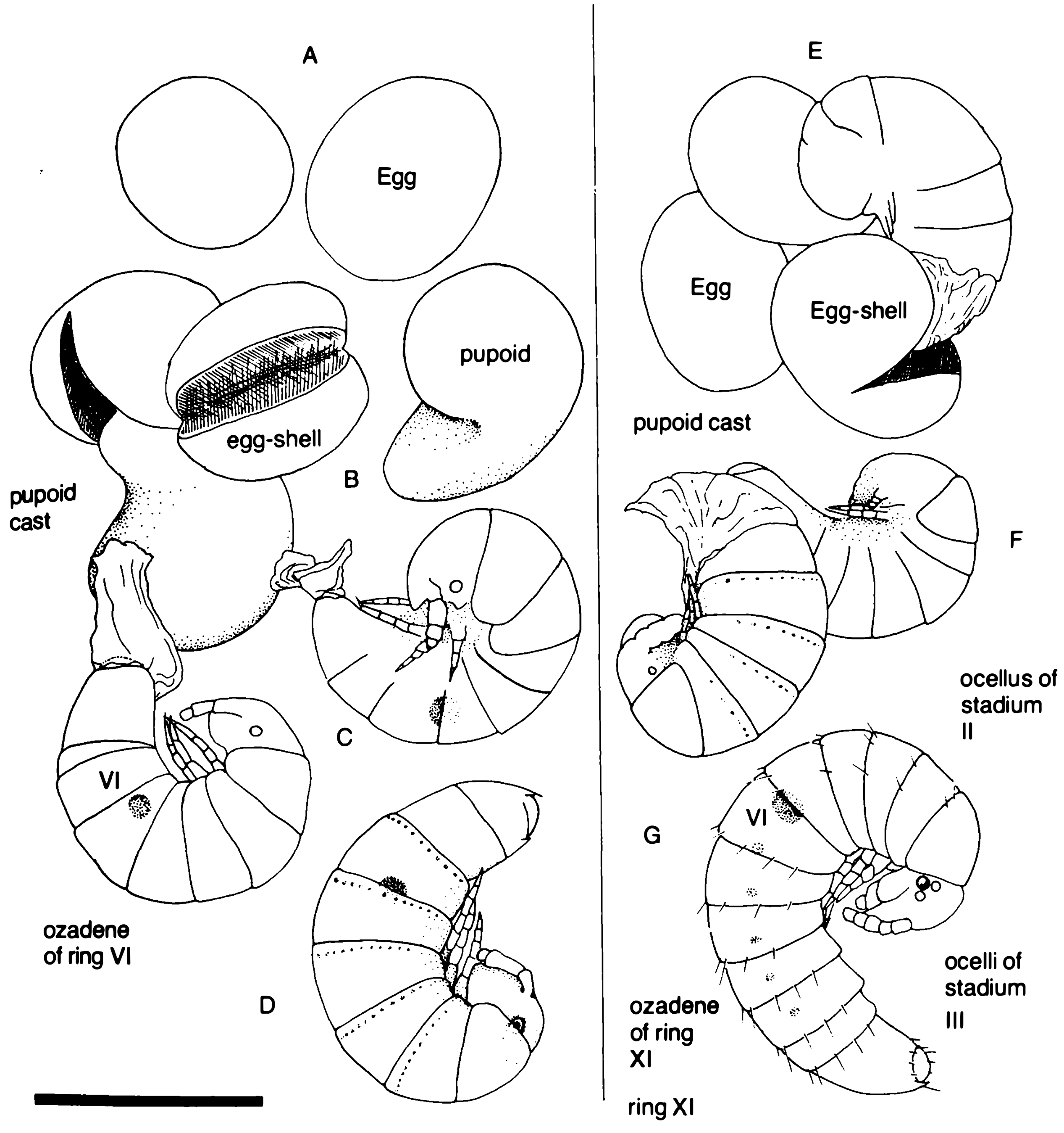


Fig. 7. Eggs, pupoids and young stadia of julids drawn from life. *Tachypodoiulus niger*: A. Eggs; B. pupoids; C. two recently moulted individuals of stadium I, with pupoid casts still adherent; D an individual in stadium I, 36 hours later than those figured at C; this larva is ready to moult into stadium II; by this time the cuticle is a delicate amber and there are orange patches of pigment around the posterior margins of the rings; the proliferation zone is extending preparatory to the moult from I to II. In C and D the single ocellus and the orange coloured ozadene on ring VI of stadium II are visible through the transparent cuticle of stadium. I. The metazonite setae are not easily visible and are not included in the drawing; *Julus scandinavius*: E. stadium I newly moulted from the pupoid and still partly enclosed in the egg shell; F. two individuals of stadium I with four podous and two apodous rings, a day later, removed from the egg shells, with the casts of the pupoids still adherent; the single ocellus of stadium II shows clearly through the transparent cuticle of stadium I. G. an individual of stadium II with six podous and five apodous rings (seven pairs of legs not all visible in the drawing); the smaller ozadenes of the apodous rings show through the ring anterior to that to which they belong; the two ocelli of the second row which will appear in stadium III can be seen through the transparent head capsule of stadium II.

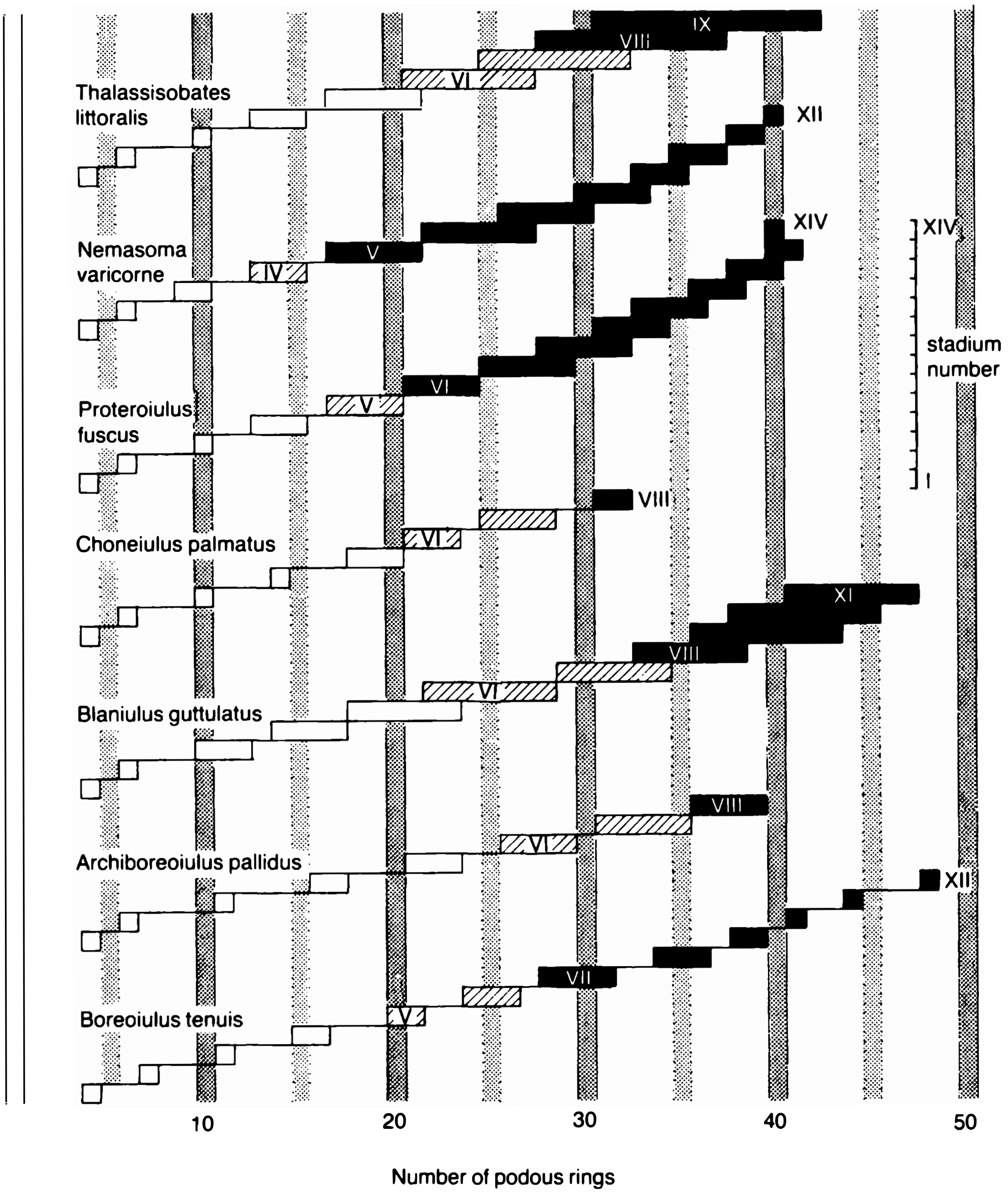


Fig. 8. Anamorphosis in Nemasomatidae and Blaniulidae. The rectangles representing stadia extend horizontally along the range of podous rings; The position of each rectangle on a vertical scale (see upper right) indicates stadium. Cross-hatched rectangles represent stadia in which sex is recognizable by absence of legs on ring VII of the male; the first sexable stadium is shown by a roman numeral within the rectangle. Black rectangles represent stadia in which adults (or intercalary males) occur; the first stadium in which maturity can be attained (usually males only in this earliest stadium), and the last, are indicated by roman numerals within the black rectangles. Note the unusual number of rings in stadium II of *Boreoiulus tenuis*.

and so on. The ocelli thus accumulate into an equilateral triangle. After a number of stadia the base of the antenna limits the number of ocelli added in the later rows; the number of rows is a fairly reliable guide to the stadium. The stadium number is obtained by adding one to the number of rows. Interpreting the ocular field depends on correctly identifying the rows (Fig. 10).

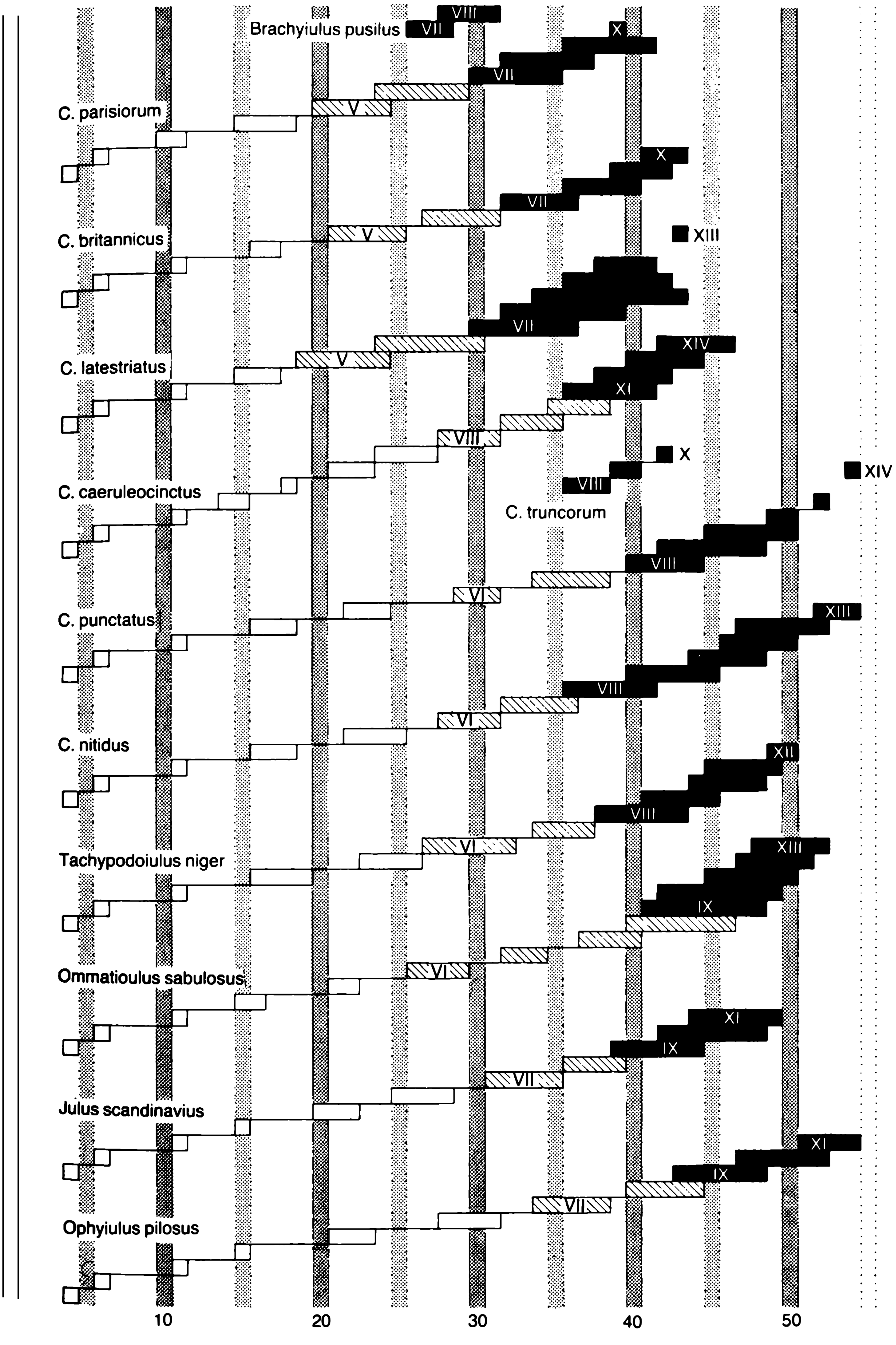


Fig. 9. Anamorphosis in Julidae: Legend, scale and conventions as in Fig. 8.

Table 1 *A tabular comparison of anamorphosis in diplopods*

Stadium	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
POLYXENIDA															
Polynexus															
tergites	5	5	6	7	8	9	10	11		followed by further epimorphic stadia.					
leg pairs	3	4	5	6	8	10	12	13							
GLOMERIDA															
Glomeris															
tergites	8	8	9	10	11	12				followed by a further nine or ten epimorphic stadia with the same segmentation as stadium VI.					
leg pairs	3	8	10	13	15	17/19									
Stygioglomeris															
tergites		8	9	10	11	12	12			followed by an unknown number of epimorphic stadia.					
leg pairs		6	8	11	14	16	17								
POLYDESMIDA															
rings	7	9	12	15	17	18	19	20							
podous	4	6	8	11	14	16	17	18		*Brachydesmus*, *Macrosternodesmus* and *Prosopodesmus* mature at VII with 19 rings. *Polydesmus* and all others mature at VIII with 20.					
apodous	2	2	3	3	2	1	1	1							
leg pairs	3	6	11	17	23	27	29	31♀							
	.	.	11	16	22	26	28	30♂							

CHORDEUMATIDA										
pleurotergites	6	8	11	15	19	23	26	28	30	
podous	4	5	7	10	14	18	22	25	27	
apodous	1	2	3	4	4	4	3	2	2	
leg pairs	3	5	10	16	24	32	40	46	50♀	All except chordeumatids
	.	.	.	.	.	.	.	44	48♂	
						.	.	46	49♀	chordeumatids except *Melogona scutellare*
						.	.	44	45♂	
					.	.	40	45♀		*Melogona scutellare*
					.	.	38	41♂		
JULIDA										
Julidae										
rings	7	11/12	16/20	20/27	*	*	⟶			Variable increments depending on species and individual up to stadium XIV or even XV. Maximum number of rings so far recorded in British Julidae = 56; minimum, 28 in *Nemasoma varicorne*, adult V; 29 in *Brachyiulus pusillus*, stadium VII; 26 in *Proteroiulus fuscus*, VI
podous	4	6	10/11	15/19	*	*	⟶			
Blaniulidae + Nemasomatidae										
rings	7/8	10/12	14/18	18/24	*	*	⟶			
podous	4	6/7	9/11	13/17	*	*	⟶			

Notes:

(1) 'Rings', 'tergites' or 'pleurotergites' = number of podous rings + number of apodous rings + telson, although the first four rings (collum plus next three) have only three pairs of legs between them, they are all regarded as podous.

(2) In Chordeumatida the last pair of legs appears to belong to the first apodous ring.

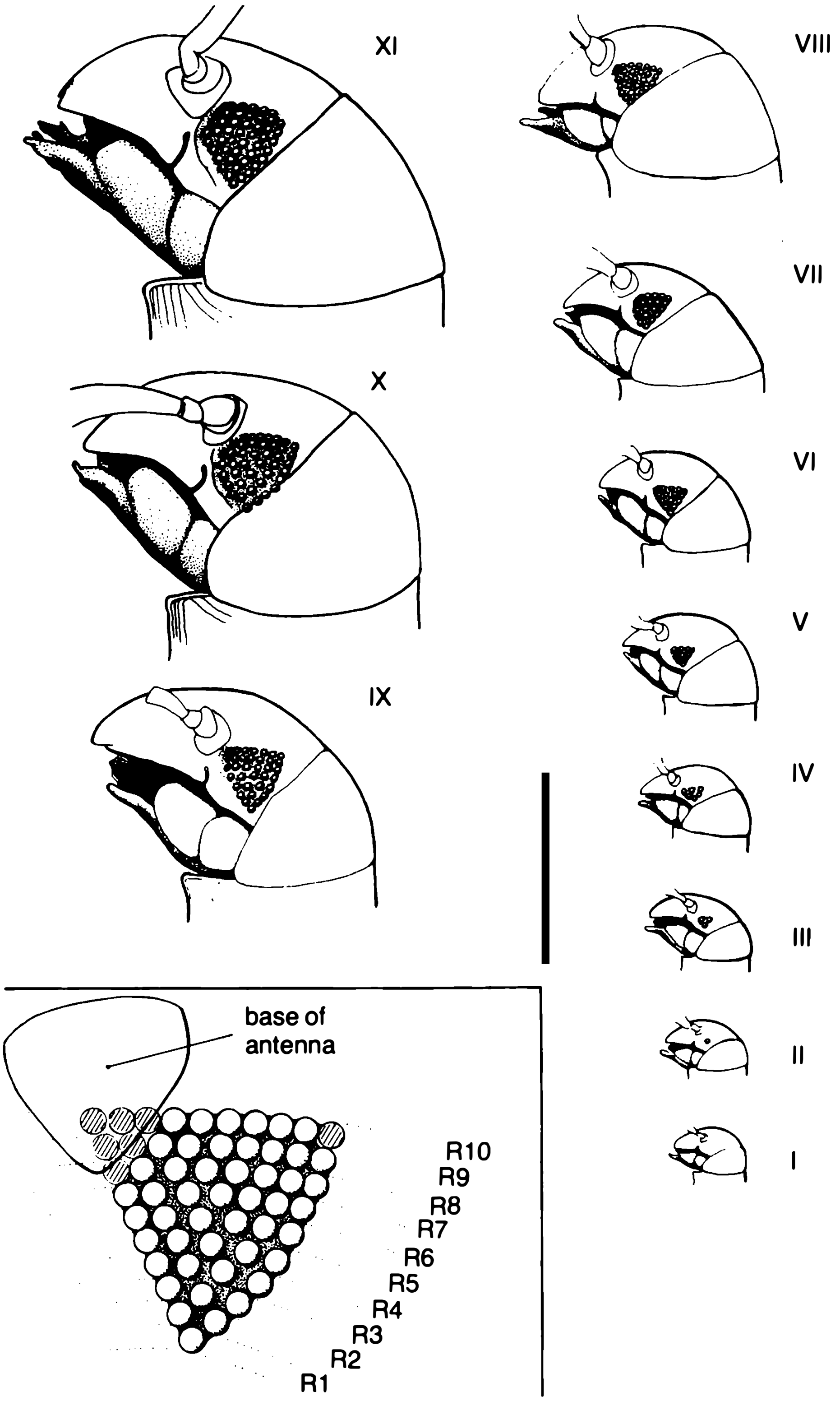


Fig. 10. Growth of the ocular field in *Julus scandinavius*. Drawings of the heads of stadia I to XI to show the arrangement of ocelli within the ocular field. The original ocellus of stadium II forms the posterior apex of the triangular field (lowermost in the figures). The most recently added row of ocelli forms the anterodorsal edge of the field (uppermost in the figures). Numbers of ocelli in the successive rows are:

Number of row	1	2	3	4	5	6	7	8	9	10
Number in row	1	2	3	4	5	5/6	7	7	7	6
Stadium	II	III	IV	V	VI	VII	VIII	IX	X	XI

Lower left is an idealised drawing to show the rows (R1 – R10) of stadium XI. The antennal base restricts the number of ocelli in the later rows. To view and interpret the field it is better to position the head as in the figures, with a top light coming from the upper left to highlight the rows.

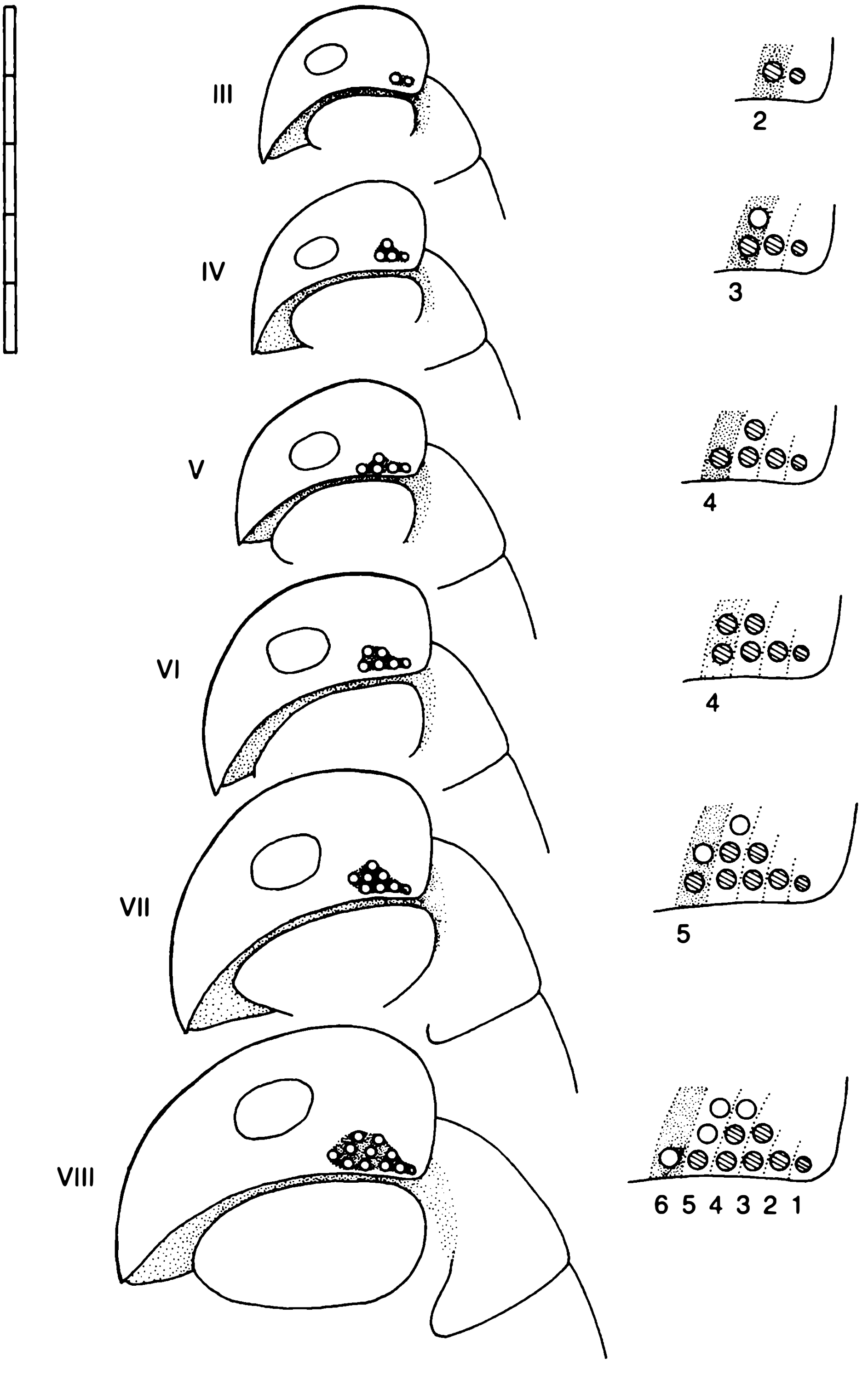


Fig. 11. Growth of the ocular field in *Melogona scutellare*. The ocular field in members of the CHORDEUMATIDA develops in a manner similar to that in the JULIDA (see Fig. 10) except that the first *two* rows are each represented by a single ocellus. There are further restrictions in *Melogona* as indicated here for *M. scutellare*. Diagrams of the ocular field are shown on the right at twice the scale of the drawings on the left. The most recently added row is indicated on the right by stipple. Arrows indicate an ocellus which has been added in a pre-existing row; ocelli invariably present are cross-hatched; ocelli not always present on one or both sides of the head, are left open.

Compare the eye rows of *Julus scandinavius* with those of *Tachypodoiulus niger* (Fig. 12), *Cylindroiulus londinensis* (Fig. 43), and with the indistinct and irregular arrangement in *Enantiulus armatus* (Fig. 52).

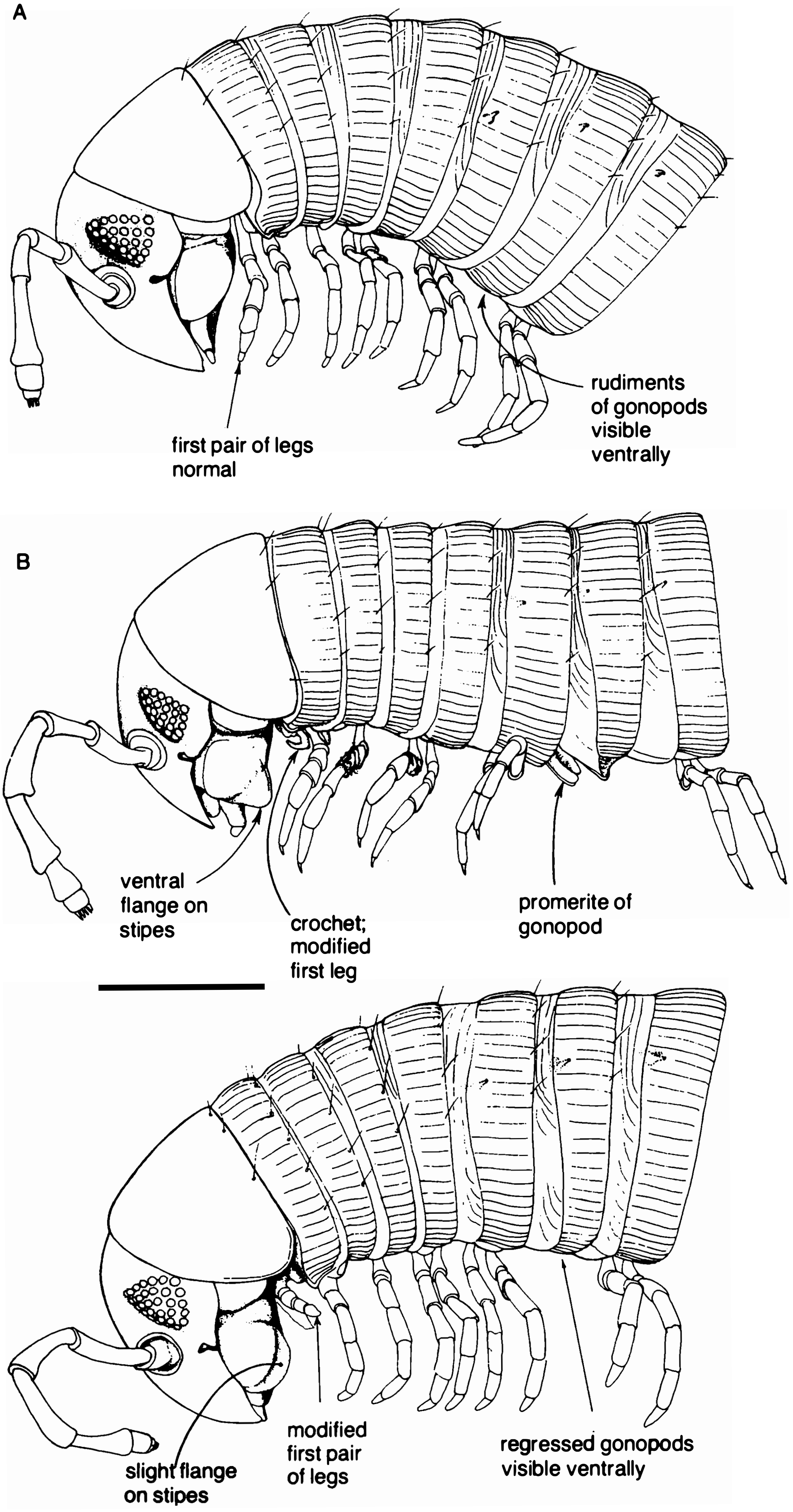
There is a similar development of the ocular field in the Chordeumatida (Fig. 11). Here only one ocellus represents the first and second rows; thereafter, the rows contain two, three, four ocelli and a triangle develops subject to the same limitations as apply in the julids.

Maturation

The last stadium in the orders Polydesmida and Chordeumatida is the adult; this is true also for some of the Julida but in this last order the stadium at which maturity is achieved is variable and the male often matures a stadium before the female. In some species of Julida there are further moults after maturity is first achieved. The first and final mature stadium of the Polydesmida is either stadium VII or stadium VIII. The final mature stadium of the Chordeumatida is either VIII or IX. In the Julida maturity is achieved in any one of the stadia V to XI and this stadium may or may not be the last. The first mature stadium *is* the last in the julines; in the cylindroiulines mature females undergo further moults; sometimes, in *Cylindroiulus nitidus* (p. 150) and *Nemasoma varicorne* (p. 102) for example, the males also moult again. In the Schizophyllini and in the Blaniulidae both males and females undergo further moults but here the sequence of male 'post-adult' stadia comprise both functional ('**copulatory**') and non-functional ('**intercalary**') stages (Fig. 12). In this modification of male anamorphosis called **periodomorphosis** the first mature 'copulatory' male usually moults into an intercalary stage where the gonopods regress to a condition somewhat intermediate between those of the juvenile penultimate stadium male and the fully formed gonopods of the 'copulatory' phase; in addition, the crochet-like first pair of legs regress also to a condition intermediate between them and the normal walking legs. At the next moult, the intercalary male may become mature again or might remain in the intercalary stage. An alternation between 'copulatory' and intercalary stages may occur but is not obligatory. In the species exhibiting this phenomenon of periodomorphosis (principally the Schizophyllini and the Blaniulidae) an adult 'copulatory' male rarely moults into another functional 'copulatory' male.

Fig. 12. Periodomorphosis in *Tachypodoiulus niger*. A. An immature male in the stadium immediately preceeding the mature male, with normal first pair of legs and rudimentary gonopods (like those in Fig. 13A); B. The mature ('copulatory') male with expanded stipes, crochet-like first pair of legs and promerites protruding through the gonopodal aperture on ring VII; C. The intercalary male which follows the mature condition after a moult and is characterised by regressed gonopods, first pair of legs intermediate in form to those of the immature and mature stages, and a slightly expanded stipes.

A and B are stadium VIII males, C is in stadium IX. The ocular fields in the drawings can be checked to ascertain this. See the text for an explanation of why these successive stages of maturity need not be present in successive stadia.


A
first pair of legs normal
rudiments of gonopods visible ventrally
B
ventral flange on stipes
crochet; modified first leg
promerite of gonopod
slight flange on stipes
modified first pair of legs
regressed gonopods visible ventrally

Sex is distinguishable before the appearance of the first mature stadium; in the males, one or both pairs of legs of the seventh ring are replaced by small gonopod rudiments and a gap is apparent where the eighth or the eighth and ninth legs should be (Fig. 13A). This gap in the series of legs of the immature male is present in the Polydesmida from stadium IV. In the Chordeumatida the gonopod rudiments appear first in the stadium immediately preceding the adult. In the Julida the gonopod rudiments from both eighth and ninth pairs of legs usually appear in the stadium but one before that in which maturity is first achieved (Fig. 13).

Moulting

Most millipedes prepare for the moult by excavating or constructing a special recess or chamber in which they lie in a loose spiral position. Chordeumatidans construct their moulting chambers from silk. A feature of the premoult condition is the extroversion of the vulvae or gonopods or their rudiments and the extension of the proliferation zone just anterior to the telson. The old cuticle splits dorsally between the head and the collum and the new stadium walks out of the old cuticle. In the Julida the rings are telescoped so that the complete cast is much shorter than the original body length. The cast skin is usually eaten by the newly moulted animal before leaving the moulting chamber.

The life cycle

Under this heading the calendar of events between a female laying eggs and her daughters laying the new generation will be followed, thus completing one cycle in the life of the species. But a female does not necessarily die after laying eggs; some females do just this but others may survive to lay again in subsequent years. In addition to knowing the time which elapses between one egg being laid, hatching, growing, maturing and laying the next generation of eggs – a knowledge of the longevity of the individual females of a given generation is also required. This may exceed the generation time by the period survived by females after their first brood, to lay further annual broods.

Time taken to reach maturity

Most British millipedes lay their eggs in the spring or early summer. Chordeumatidans lay their eggs in early spring or even in the winter. Only a few small species achieve maturity in time to lay eggs in the year following that of their birth, for example, the chordeumatid *Melogona scutellare* (p. 94) and the small polydesmid, *Brachydesmus superus* (p. 206). Most millipedes need at least one year and six months to achieve maturity in the second autumn after their birth. For examples, the julids *Ophyiulus pilosus* (p. 172)

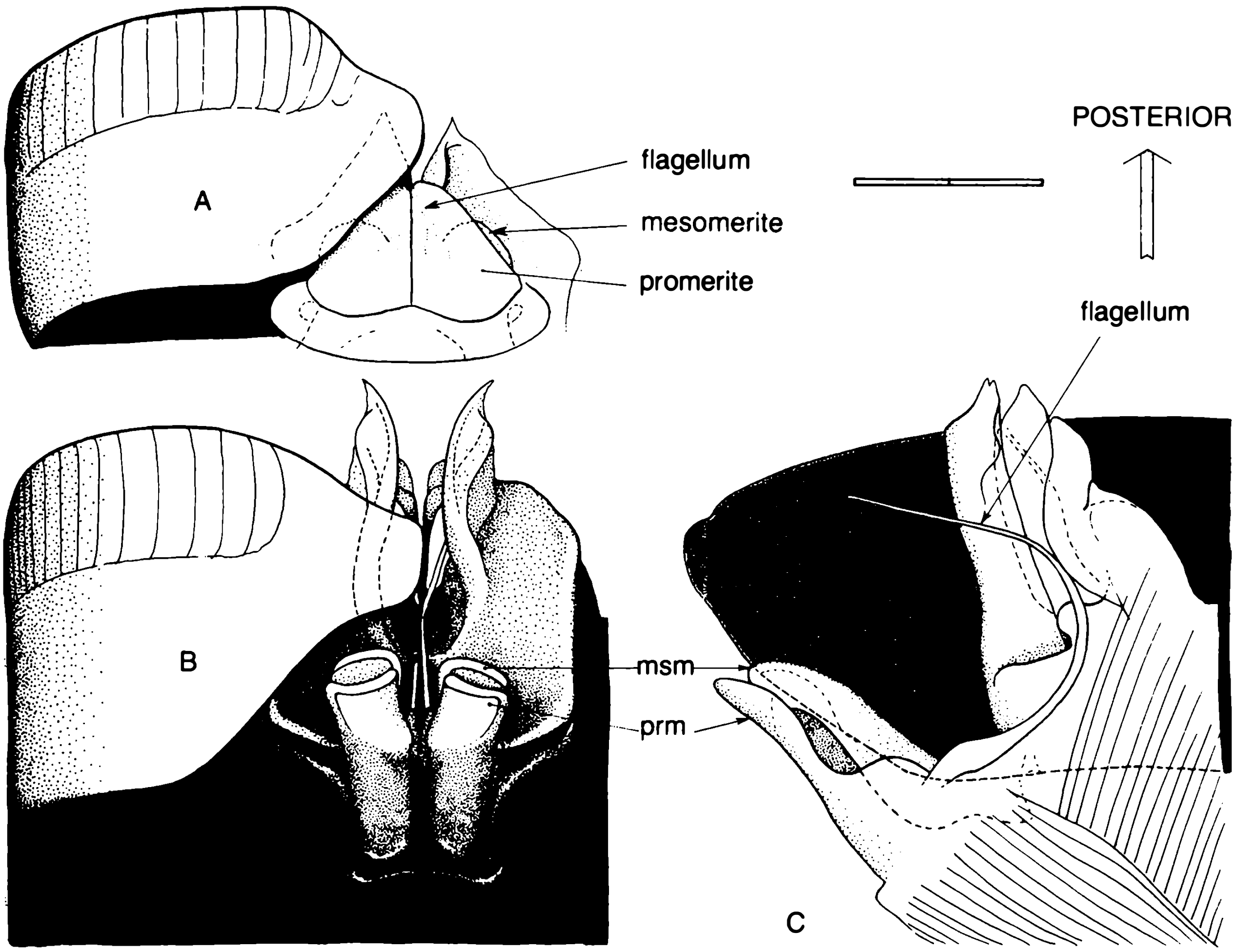


Fig. 13. Gonopods of a julid, *Cylindroiulus latestriatus*. A. The embryonic gonopods of the stadium immediately preceeding the mature male, ventral view with right pleuro-tergal lobe removed; B. Fully-formed gonopods of the adult male, ventral view with right pleuro-tergal lobe removed; C. Lateral view of B with right gonopods removed to show left gonopods in mesial profile. The promerites effectively close the gonopodial aperture and are normally the only parts of the gonopods visible in ventral view. During pairing with a female the entire gonopodal apparatus is everted (from Blower & Gabbutt, 1964): *msm*, mesomerite; *prm*, promerite.

and *Cylindroiulus latestriatus* (p. 155), the nemasomatid *Nemasoma varicorne* (p. 102), are able to oviposit two years after their birth, whilst the julids, *Julus scandinavius* (p. 168), *Tachypodoiulus niger* (p. 135) and *Cylindroiulus punctatus* (p. 152), the blaniulid *Proteriulus fuscus* (p. 107) and the pill millipede *Glomeris marginata* (p. 58) reach maturity in the third antumn after their birth and oviposit in their third spring. *Cylindroiulus nitidus* (p. 150) takes four years to reach maturity.

Longevity: survival to lay further annual broods

In the Polydesmida, the Chordeumatida, and the common Julida of the tribe Julini (*Ophyiulus pilosus* (p. 172) and *Julus scandinavius* (p. 168) females and males die after reproduction and there is a period between the death of the parents in late spring or summer and the arrival of the new generation of adults the following autumn when no adults are to be found. This 'breed and die' strategy is called **semelparity** (single breeding). Females of the pill millipede *Glomeris marginata* (p. 58) and many julids and blaniulids survive after laying their first brood to lay further broods in the following year or years. There is no time in the year when the populations of a species laying successive annual broods do not contain adults. This habit is called **iteroparity** (= repeated breeding). The longevity of such species is considerably extended. *Glomeris marginata* females maturing first at three years old survive to lay up to seven or eight further annual broods up to the age of 10 or 11 years old. *Tachypodoiulus niger* (p. 135), also maturing at three years old, may continue for a further four, five or six years.

Male cycle

The females are usually credited with the completion of the life cycle and the ability to survive their first egg laying and live to a ripe old age. There are those species exhibiting parthenogenesis where this is indeed true. Most species however, find males necessary although they are frequently less numerous than the females. Males of most cylindroiulines do not moult after achieving maturity and do not survive their first period of reproduction. Since females of this tribe survive their first brood to moult again and breed in several more years it follows that the sex ratio will be biased towards females. The males of schizophyllines survive their first breeding season for a number of years by virtue of the periodomorphosis previously described, but since two moults are necessary in between each annual breeding season the hazards to survival appear to be doubled. Mortality of males is therefore greater than of females and the sex ratio is still more biased in favour of females although not as markedly as in the cylindroiulines. Only in *Cylindroiulus nitidus* (p. 150) can males survive along with the females, on the same terms, so-to speak, copulatory moulting into copulatory stage without the intervention of intercalaries. In this species the sex ratio most closely approaches one to one.

Males are often smaller than the corresponding females and can mature in a shorter time. This is especially true of males of the Julida. In this order the males may mature a year earlier than the females; males of the pill millipede *Glomeris marginata* and the julid *Tachypodoiulus niger* may mature in two years whilst the females take three. Males in the Polydesmidae are usually larger than the females.

Stadial and age structure of populations

From the foregoing account it might be tempting to construe the occurrence of several different stadia of mature animals in a population as indicative of the iteroparous habit; it might be thought that the different stadia represented different generations. But since the stadium in which maturity of julids is first achieved is variable, so might the year in which maturity is achieved also be variable. A series of different stadia of adults does not necessarily indicate successive years of maturity. In particular, the presence of mature males in several stadia does not necessarily mean a sequence of male moults; these are only known in *Cylindroiulus nitidus* (p. 150) and those species exhibiting periodomorphosis. In *Cylindroiulus punctatus* (p. 152), for example, there can be males in stadia VIII, IX and X but each has arisen from a juvenile of the preceding stadium. Males of stadia VIII and IX may have matured together in the same year and represent the same generation; some of stadium IX, and stadium X may have arisen from an earlier generation, having remained immature in stadia VIII and IX and taken a year longer to mature.

Whilst it is relatively easy to derive the stadial structure of a population, the translation of this structure into age structure can only be achieved by sampling the population at intervals over a period of at least one year.

Movements

Millipede movements have been analysed, along with those of other arthropods in the now classic series of papers by Dr. S. M. Manton entitled 'The Evolution of Arthropod Locomotory Mechanisms' (1950, 1952a, b, 1954, 1956, 1958, 1972 and 1973; and resumé in 1977). Much of what follows is drawn from part 4 of this series (1954), and is best introduced by her own words: 'A marked ability to push is as diagnostic of the Diplopoda as the possession of diplosegments. This and the ability to curl the body into a tight or loose spiral are two major habits ... of major importance in the evolution of the structural peculiarities of the group.'

The ability to push

The push is delivered by the motive force of the legs; the more legs, the bigger the push. The animals use a low gear gait; the legs spend a greater part of the time on the ground propelling than off the ground recovering; the two legs of a pair are always in the same phase. In the juliforms the push is delivered to the substrate by the collum which acts like the blade of a bulldozer. In the polydesmids and the craspedosomatids the push is delivered by the flat backs; in these orders the head end of the body is narrower than the mid-trunk region; the animal insinuates its head end into a crack and the flat backs then widen the crack rather like a mobile wedge. In transmitting the force of the legs to the substrate via collum or paranota it is of course essential that the trunk does not shorten in the process.

Spiralling

Curling into a spiral or enrolling into a sphere depend on the flexion of one ring about another. To facilitate this flexure the rings articulate by what are in effect, ball and socket joints; the trunk is thus comparable to a spinal column of opisthocoelous vertebrae. Like the vertebral column, the trunk is designed to resist shortening when all the legs contribute to the push and yet retain the necessary flexibility to allow the spiral reflex. The inter-ring joint and its flexor and stabilizing muscles is a complex affair; the economic device of engineering just one joint per two pairs of legs is the *raison d'etre* of diplopody itself.

The fulcra about which two adjacent rings flex in the vertical plane are mid-lateral; because of this, the completeness of the spiral depends on the ventral halves of the rings packing up neatly against each other. The fulcra of a pill millipede are ventro-lateral; the ventral pleurites and sternites are on the axis of flexure and there is no 'taking-in' problem; the animals achieve a perfect sphere on flexion. Some millipedes such as the spotted snake, *Blaniulus guttulatus* (p. 116) curl into a perfect plane spiral; the julines *Ophyiulus pilosus* (p. 172) and *Julus scandinavius* (p. 168) form a helical spiral. Spiralling is not always the initial reaction to disturbance. Some species react to danger by rapid flexion and extension of the body or by sinuous movements as in *Ophyiulus pilosus*, appropriately named *the* snake millipede. *Polydesmus* and its allies do not spiral as a defensive measure but freeze motionless when disturbed.

Spiralling is often accompanied by the discharge of material secreted by the ozadenes when the millipede is attacked by a predator (p. 34). The two schizophyllines are the most likely to discharge their ozadenes when handled by the collector. *Ommatoiulus sabulosus* (p. 131) with its colourful dorso-lateral orange stripes, and *Tachypodoiulus niger* (p. 135), with white legs contrasting with black body are our two most conspicuous julids. It seems reasonable to interpret this conspicuousness as an example of warning colouration or aposemosis.

Discharge of the glands by polydesmids is rarely noticeable when the animals are handled. Their rather drab colouration and their protective behaviour of freezing motionless when disturbed are more suggestive of crypsis than aposemosis. Possibly the ozadenes in this family may serve some other function such as fungistasis. However, many exotic polydesmidans are strikingly coloured as are our British paradoxosomatids.

Speed, susceptibility and activity

Speed is not consistent with the low gear gaits employed by millipedes, nor is speed to be expected of animals moving through soil and litter. Nevertheless, not only are some faster than others, a few could almost be described as fleet. The fastest julid is the appropriately named *Tachypodoiulus niger* (p. 135). A medium sized adult of this species walks at 13 mm per second. An individual *Polydesmus angustus* (p. 194) of the same weight is about 50% faster than the julid, but the really fleet millipedes are the Chordeumatida. *Nanogona polydesmoides* (p. 74), for example, is 33–50%

faster than a *P. angustus* of similar weight. *Melogona scutellare* (p. 94), one third the length and one fiftieth the weight of the medium *T. niger* mentioned above, walks at roughly the same speed (Manton, 1954). Fleetness is possibly associated with greater susceptibility to adverse moisture and temperature regimes. Chordeumatida are certainly the most difficult millipedes to rear in captivity.

It is important to note that various speeds of surface activity will lead to certain species falling into pitfall traps in greater numbers. In particular, males are invariably more active than females and are disproportionately represented in traps.

Feeding

Most millipedes are detritivores, eating dead vegetation such as woodland leaf litter and dead wood, preferably leaves and wood which have been on the ground for some time and have undergone some microbial decomposition, Julids such as *Julus scandinavius* (p. 168) and *Ophyiulus pilosus* (p. 172) have been reared in the laboratory from egg to adult on a diet of dead leaves alone (Kheirallah, 1966; Blower, 1974a). Certain types of leaf litter are more palatable than others (Kheirallah, 1979). One of the earliest investigations into the feeding habits of soil detritivores was that of Lyford (1943) who established that *Cylindroiulus caeruleocinctus* (p. 144) preferred leaves with the higher content of calcium. Later work revealed that preferred leaves such as ash and elm with higher calcium content were also relatively richer in nitrogen and contained no phenolic materials, or relatively small quantities of these and were consequently subject to more rapid microbial decomposition. At the other end of the scale, leaves such as oak and beech which are poor in calcium, have relatively less nitrogen, more phenolic material and decompose more slowly, so not surprisingly newly fallen leaves of these species are unpalatable to millipedes.

Millipedes are not well equipped with specialized enzymes to enable them to digest the leaf material itself. It is suspected that they rely on the food material elaborated by the microorganisms in their bodies rather than the microbially degraded leaf material. Some millipedes (Chordeumatida, for example) may browse directly on fungal hyphae or fructifications, selecting them before ingestion instead of *en route* down the gut from a pabulum of dead leaf or wood material.

Millipedes habitually feeding on litter may be important agents in the process whereby plant debris falling onto the soil surface is comminuted and ultimately converted into humus. Their role in this process is considered to be largely mechanical as they appeared to assimilate rather a low proportion of the material they ingest. More recent work on several species of millipedes has produced estimates of assimilation efficiency ranging from 5% to 50% (Kayed, 1978). If the assimilable material is mainly the contained microorganisms their overall effect could still be largely mechanical whether their assimilation efficiency be high or low. It is perhaps more useful to ascribe their limited chemical effect to the apparent absence of specialized digestive enzymes.

The more subterranean species such as the poorly pigmented blaniulids and the moderately pigmented species of *Cylindroiulus* (p. 139) sometimes have quantities of soil in their guts. It is not known whether such intake is incidental to a diet of dead root material or for the purpose of extracting amorphous organic material. The surface active species such as *Julus scandinavius* (p. 168) and *Tachypodoiulus niger* (p. 135) occasionally have unicellular algae in their guts. The frequent excursions of the species up onto tree trunks may be for the purpose of browsing on epiphytes such as *Protococcus*.

Millipedes take living plant material on occasion, particularly the delicate rootlets of seedlings (see next section). There are reports of *Blaniulus guttulatus* taking animal matter.

Economic aspects

Millipedes are frequently suspected of attacking crop plants. The spotted snake millipede, *Blaniulus guttulatus* (p. 116), probably owes the distinction of having a common name to the frequency with which it is encountered by farmer and gardener. Together with other species of blind blaniulids and the small pale *Brachydesmus superus* (p. 206), these animals are often found in roots and partly hollowed-out potato tubers. It is generally assumed that the millipedes in such situations are merely aggravating damage initiated by some other agent. Recently, the habit of sowing monogerm sugar beet has apparently lead to depredations by blaniulids which have been taken more seriously. The millipedes have been credited with the initial damage which has sometimes proved economically disastrous.

Another group of millipedes impinge on everyday human activity in a different manner. These are the julids of the tribe Schizophyllini which display a larger horizontal and vertical range of movement than other millipedes. *Tachypodoiulus niger* (p. 135) and *Ommatoiulus sabulosus* (p. 131) occasionally group together in their movements and sometimes enter dwellings in large numbers. Afflicted householders can be assured that the invading millipedes present no sinister threat but merely constitute a nuisance.

Chemical defence

As early as 1882 the production of hydrocyanic acid by a millipede was reported; in 1900, a quinone was found to be the active principle in the secretion of a julid and the striking smell of camphor from *Polyzonium* (p. 66) had been noticed. However, it was not until the last two decades that the ozadene secretions were chemically characterized in a wide variety of species. The pioneering work and all the later discoveries in chemical ecology of millipedes have recently been reviewed in an excellent account by Professor Eisner and his colleagues who have been closely involved with much of the work (Eisner *et al.*, 1978).

Juliform orders are referred to as the 'quinone millipedes'. The principal components are two benzoquinones; they have been characterized in *Ommatoiulus sabulosus* (p. 131), *Cylindroiulus caeruleocinctus* (p. 144) and *Blaniulus guttulatus* (p. 116) amongst other julidans, spirobolidans and spirostreptidans. The Polydesmida is called by Eisner and his colleagues the 'cyanogenetic order'. Hydrocyanic acid (with benzaldehyde) is produced by the dissociation of a cyanohydrin, mandelonitrile, in most of the Polydesmida examined although the only British representative in their survey is *Oxidus gracilis* (p. 218). *Glomeris marginata* (p. 58) secretes two quinazolinones, glomerin and homoglomerin. Although alkaloids are well known as secondary metabolites in plants, these alkaloids secreted by *Glomeris* are the only known quinazolinones produced by an animal. The secretion produced by *Glomeris* also contains proteinaceous material and is viscous and sticky whereas that in juliforms and polydesmidans is a mobile fluid without macromolecules. The secretion of the ozadenes of *Polyzonium* is also white and sticky; it is not camphor but consists of the monoterpene polyzonimine and the closely related nitropolyzonamine. No monoterpenes of natural origin have a similar structure; these secretions of *Polyzonium* are compounds which do not have close relatives among the secondary metabolites of plants.

Eisner *et al.* (1978) also describe the effects of these various chemicals on attacking predators. The quinones and polyzonimine act mainly as repellents; cyanide, of course, as a toxin. All may have an initial irritant effect and act as deterrents, and prove toxic on ingestion. Presenting pure quinone or polyzonamine to ants feeding at sugar caused them to disperse within seconds. The alkaloids from *Glomeris* caused death when ingested by mice; toads vomited the animals and spiders developed motor impairment or even total paralysis hours after attacking a pill millipede. The viscous secretion pulls out into threads which harden on exposure and cause entanglement of predators. Nevertheless, as Eisner *et al.* point out, there are several animals known to feed on millipedes (p. 36), including a mysterious animal which takes just the head and first five rings of an American spirobolid, thereby avoiding the ozadenes. The responsible animal is not yet known but is referred to by Eisner and his colleagues as Robespierre.

An unusual example of the second hand use of the ozadene secretion of *Glomeris marginata* (p. 58) was described recently (Thomas, 1982). She describes the occasion she saw a robin pick up a pill millipede and annoint the undersides of the primary feathers of each wing in turn, several times, before releasing the millipede. This must be the first report of a bird 'anting' with a millipede; the ozadene alkaloids must be every bit as effective as formic acid.

Predators and parasites

Although I have occasionally found *Tachypodoiulus niger* (p. 135) in the meshed webs of *Amaurobius* (= *Ciniflo*) spp. and Bristowe records *Meta menardi* in a cave, eating a *Polydesmus* sp., there are few records in Britain of invertebrate predation. Snider (1981a) records predation by carabid beetles in both the field and in the laboratory in Michigan, U.S.A. The millipede prey were two of our species which have been introduced into the U.S.A., *Polydesmus inconstans* (p. 200) and *Ophyiulus pilosus* (p. 172). In the laboratory beetles were reared through larva, pupa and adult on these millipedes. Most recorded instances of predation have involved vertebrates. In the United States starlings have been reported to feed almost exclusively on the introduced *Cylindroiulus caeruleocinctus* (p. 144) in the spring months and millipedes have been recorded in the guts of British starlings. Song thrushes might be expected to be important predators, also blackbirds which sort through leaf litter in a similar manner to the millipede collector. Blackbird, song thrush, mistlethrush and redstart are all known to take millipedes but there are no quantitative studies.

Both julid and polydesmid millipedes are found in the stomachs of frogs and toads and there are records of urodeles and lizards feeding on millipedes. Whilst the reported absence of millipedes from the guts of shrews may testify to the effectiveness of the ozadenes, their secretion appears not to deter hedgehogs for which millipedes form a significant but small part of their diet (Yalden, 1976).

The most frequently encountered metazoan endoparasites are nematodes of the genus *Mermis*. In dissecting large numbers of our common julids for eggs I have occasionally noticed worms three times the length of the millipede folded into the space that should have been occupied by eggs; but the incidence of these parasites is very small. Larvae of muscid flies have been reported as have cestode cysticercoids but I have not encountered them. By contrast, infestation by cephaline gregarines is rather common.

Species of the 'luscus' group of *Cylindroiulus* (p. 139) are fairly frequently attacked by ectoparasitic fungi of the Laboulbeniales. The branched hyphae are usually found in adults attached to the first three pairs of legs of the female or to the first seven pairs of males; perhaps the animal is unable to groom these legs effectively; then again, the absence of ozadenes from the first five rings might be a factor.

The enemies of millipedes have been listed and reviewed by Cloudsley-Thompson (1949), Remy (1950) and Eisner *et al.* (1978).

Habitat preferences

The majority of millipedes live at the interface of the soil and the litter layer on which many of them feed. They make excursions deeper into the soil when the need arises – for moulting or egg-laying or to avoid winter cold or summer dryness. A few make excursions above the soil surface and climb trees and walls when night falls and humidity rises. The two schizophyllines, *Ommatoiulus sabulosus* (p. 131) and *Tachypodoiulus niger* (p. 135) are the specialist tree and wall climbers and they occasionally fall onto the beating tray to surprise the collector seeking quite different animals. Several others, usually the well-pigmented species, frequently walk about on the surface at night and can be collected in pitfall traps. The lighter the pigment, the less likely is the species to leave the protection of the litter or other surface debris. The pale blind blaniulids, the relatively pale *Cylindroiulus nitidus* (p. 150) and the small pale species of the Polydesmida could be described as subterranean in habit.

All species may be found on occasion under stones and fallen logs but usually it is the well-pigmented, surface active species which use these refuges during their inactive phase. Under the bark of tree stumps and logs are spaces providing good refuges for surface active species and here there is a food supply so several species live most of their lives here and in the decaying wood underneath. Examples of these sub-cortical and dead wood species are the julids *Cylindroiulus punctatus* (p. 152), *C. britannicus* (p. 158) and *C. parisiorum* (p. 160), the well-pigmented blaniulid, *Proteroiulus fuscus* (p. 107) and the nemasomatid, *Nemasoma varicorne* (p. 102).

The greatest variety are to be found in woodland where up to a dozen species and densities of up to 850 per square metre are recorded from small areas. But several species extend their range into arable and grassland, notably *Cylindroiulus caeruleocinctus* (p. 144) and the blind blaniulids such as *Blaniulus guttulatus* (p. 116) and the small pale *Brachydesmus superus* (p. 206). The characteristic dead wood species *C. punctatus* and *P. fuscus* together with *Polydesmus angustus* (p. 194) are to be found in quite acidic woodland. Notwithstanding, the latter are the most frequently recorded species in Britain. Most species prefer base rich or limestone woods. The julids *Cylindroiulus caeruleocinctus* and the blind blaniulids *Archiboreoiulus pallidus* (p. 118) and *Boreoiulus tenuis* (p. 120) are rarely found away from calcareous soils. The acid tolerant species might be more usefully characterized as preferring sandy soils and liable to extend into conifer woods. In which case the appropriately named *Ommatoiulus sabulosus* should be added to the list. Similarly, the base-rich category might be more pertinently associated with clay or loam soils.

Several species appear to be abundant in what may be termed the marginally halophile category. *Cylindroiulus latestriatus* (p. 155) is almost confined to the coast and is common on Marram dunes. Just one species, *Thalasisobates littoralis* (p. 100) is adapted for life between tidemarks and is found at, or even below mean high water neaps where it is subject to periodic submersion by salt water.

Table 2 *Widespread and rare species*

	Number of vice-counties				Rank			
	Total	E + W	Sc	Ir	Total	E+W	Sc	Ir
	152	71	40	40				
Cylindroiulus punctatus	143	72	36	35	1	1	1	2
Ophyiulus pilosus	132	62	32	38	2	8	4	1
Polydesmus angustus	131	69	35	27	3	3	2	6=
Tachypodoiulus niger	130	71	30	29	4	2	5=	4=
Nanogona polydesmoides	124	67	28	29	5	4	8=	4=
Proteroiulus fuscus	117	63	29	25	6	6=	7	9
Brachydesmus superus	114	63	24	27	7	6=	10	6=
Glomeris marginata	112	66	14	32	8	5	13	3
Julus scandinavius	99	54	30	15	9=	10	5=	13
Ommatoiulus sabulosus	99	51	34	14	9=	11	3	14
Blaniulus guttulatus	93	58	15	20	11	9	12	11
Cylindroiulus latestriatus	88	38	28	22	12	16	8=	10
Brachyiulus pusillus	72	37	17	18	13	17	11	11
Polydesmus inconstans	68	39	12	17	14	15	11	12
Polydesmus denticulatus	62	48	6	8	15=	12	17	17=
Polydesmus gallicus	62	36	.	26	15=	18	.	8
Cylindroiulus britannicus	62	41	9	12	15=	14	16	15
Nemasoma varicorne	56	44	11	1	18	13	15	24=
Craspedosoma rawlinsii	38	16	13	9	19=	25=	14	16
Polyxenus lagurus	38	30	5	3	19=	19	18=	20
Cylindroiulus caeruleocinctus	35	29	1	5	21	20	22=	19
Boreoiulus tenuis	29	16	5	8	22	25=	18=	17=
Melogona scutellare	27	25	1	1	23	21	22=	24=
Ophiodesmus albonanus	23	22	1	.	24	22	22=	.
Archiboreoiulus pallidus	22	19	1	2	25	23=	22=	21=
Macrosternodesmus palicola	20	19	1	.	26	23=	22=	.
Cylindroiulus nitidus	18	14	4	.	27	28	20	.
Oxidus gracilis	15	11	2	2	28=	29=	21=	21=
Melogona gallica	15	15	.	.	28=	27	.	.
Choneiulus palmatus	12	11	.	1	30	29=	.	24=
Cylindroiulus londinensis	10	8	1	1	31	33=	.	24=
Cylindroiulus parisiorum	9	9	.	.	32=	31=	.	.
Chordeuma proximum	9	9	.	.	32=	31=	.	.
Stygioglomeris crinata	8	8	.	.	34	33=	.	.
Brachychaeteuma bradeae	6	6	.	.	35=	35=	.	.
Polydesmus testaceus	6	6	.	.	35=	35=	.	.
Brachychaeteuma melanops	6	6	.	.	35=	35=	.	.
Stosatea italica	6	4	.	2	35=	40=	.	21=
Leptoiulus kervillei	6	6	.	.	35=	35=	.	.
Thalassisobates littoralis	5	5	.	.	40	39	.	.
Cylindroiulus vulnerarius	5	4	.	1	40	45=	.	24=
Brachychaeteuma bagnalli	4	3	.	1	42=	42=	.	24=
Leptoiulus belgicus	4	4	.	.	42=	40=	.	.
Metaiulus pratensis	3	3	.	.	44	42=	.	.
Polyzonium germanicum	2	2	.	.	45	44	.	.
Chordeuma silvestre	1	1	.	.	46=	45=	.	.
Eumastigonodesmus boncii	1	1	.	.	46=	45=	.	.
Enantiulus armatus	1	1	.	.	46=	45=	.	.
Adenomeris gibbosa	1	.	.	1	46=	.	.	24=
Prosopodesmus panporus	1	1	.	.	46=	45=	.	.
Cylindroiulus truncorum	1	1	.	.	46=	45=	.	.

The British Myriapod Survey

In 1971 a habitat recording scheme for British Myriapoda was launched (Fairhurst & Barber, 1972; Barber & Fairhurst, 1974). As a consequence the available number of vice-county records has nearly doubled. I am grateful to Dr. Fairhurst for providing lists of this new information which has enabled me to up-date the distribution maps. The records are processed and stored at the Biological Record Centre, Monks Wood, and can be retrieved as 10 km squares or even smaller units. In addition to a full grid reference, on each card there are detailed habitat data. A preliminary analysis of these has already been made (Fairhurst & Armitage, 1979), maps of 50 km records have been circulated to members of the British Myriapod Group by Dr. Fairhurst at the 1983 meeting and a provisional Atlas will be published shortly. In the meantime, distribution in this *Synopsis* is mapped by vice-county and indicated by VC followed by the vice-county number, e.g. VC 16 = West Kent.

Table 2 summarizes the vice-county records at the end of 1980. The species are ranked according to the number of vice-counties they occupy and comparison may be made with a similar table drawn-up at the end of 1969 (Blower, 1972). As more and more records are gathered, this method of assessing commonness and rareness will become less satisfactory and will begin to emphasize range rather than abundance. At this stage the actual number of records within a vice-county or smaller area could be used to measure abundance with greater precision. In addition, a more ambitious analysis of 10 Km or even 1 Km square records will complement analysis of habitat data on the cards and allow correlation with floristic, pedological and geological features as Kime (1978) has done for an area in the south east and others are attempting in their own areas.

Readers wishing to contribute to the survey should write to: Mr. Douglas T. Richardson, 5 Calton Terrace, Skipton, North Yorkshire BD23 2AY.

Species are ranked according to the number of vice-counties in which they have been recorded.
E = England, I = Ireland, Sc = Scotland and W = Wales.

Collection, preservation and examination

General collections are made by looking under stones and logs and carefully examining both exposed soil surface *and* the underside of the stone or log, also by sorting through leaf litter until the soil surface is reached and then examining the soil and superficial root system and removing the bark from fallen logs and stumps. Quantitative collections can be made by taking a small area of leaf litter or soil (about a square foot or one tenth of a square metre at the most) and extracting the animals by sieving or by Tullgren funnel. Pieces of bark, dead wood or moss of determined size may be treated in a similar manner.

Pitfall traps consisting of a jam jar or plastic cup sunk into the soil flush with the surface secure excellent catches of millipedes (along with carabid beetles, centipedes and a whole host of other surface active animals). Potassium dichromate solution in the trap preserves the contents, prevents undue predation and yet has no vapour which may repel animals. The catch depends on the activity of the animals and care must be taken if estimating density from the results. Small species and young stadia of larger species need be sought with the eye close to the substrate and a camel hair brush or a piece of plant stem used to transfer them to the collecting tube. The safest way to secure specimens in good condition is to transfer them, together with plenty of surrounding substrate, to a large vessel or plastic bag, postponing final sorting until a good light and a firm table are available. In transporting such live material back to the lab it is essential to keep the container well sealed to conserve moisture (oxygen is not a problem since rarely is an air-tight seal achieved).

For the study of live material, a petri-dish with a covering of 1% agar gel is ideal for producing the very necessary humidity and pieces of leaf material can be smoothed onto the agar surface for food. Millipedes kept in a transparent plastic sandwich box on a layer of moist sieved soil in the spring will build their nests against the bottom of the box where they can be seen through the plastic wall. Males should be removed when a nest appears otherwise they will consume its contents. Millipedes can be examined alive most conveniently by placing them in an optically-fair glass tube, lined with a neat rectangle of moist filter paper and closed by an ordinary cork. The tube can be held with the cork on which the animal walks and rotated in front of a lens held in the other hand.

The most useful preservative is 70% alcohol to which 5% by volume of glycerine is added. The glycerine provides an insurance against complete evaporation of the alcohol and also keeps the specimens more supple.

Examination for the purpose of diagnosis is conveniently performed in a petri-dish of alcohol with the subjects completely immersed. Millipedes die partly flexed and their stable position in the dish is on their side. Accordingly, most illustrations in this synopsis are lateral views of the animals in their customary position of rest. This lateral position can be most exasperating when there is need to examine or dissect out ventrally placed structures. These operations are best performed on isolated sections of the animal which can be poised, ventral side uppermost and held by forceps or mounted needle inserted into the open lumen of the ring. Small glass beads in the bottom of a solid watch glass are useful to maintain sections of the body in unstable positions whilst drawing.

Sufficient detail in isolated gonopods, vulvae etc. can be seen with the part resting on the bottom of a dish but if orientation is difficult or the parts are small it is better to mount them on a cavity slide in 60% lactic acid. The objects can be rotated by carefully sliding the coverglass over the cell. Lactic acid remains in equilibrium with atmospheric moisture and a mount will keep for weeks; it is necessary to cover the preparation to keep dust off the surface of the coverglass.

Incident or top light is desirable for most purposes but a stage dissecting microscope with facility for transmitted light in addition to top light is useful to sharpen up the image of telson projection or fringing setae.

Measurement

Since most investigation must be of fixed, fully contracted specimens, all measurements in this *Synopsis* of length are made from such fully contracted adult animals. Specimens extended by uptake of water either before or after death are excluded from measuring. Animals are drawn in profile silhouette using a squared eye-piece and the drawings measured along the mid-lateral line by means of a map measurer.

The measurements which follow the lengths in the species descriptions are *either* breadths *or* diameters.

Breadths are given for *Polyxenus*, pill millipedes, *Polyzonium* and flat-backed Chordeumatida and Polydesmida; these are the *horizontal* measures of the widest expanse as seen in dorsal view (e.g. between paranotal extremities of flat-backs).

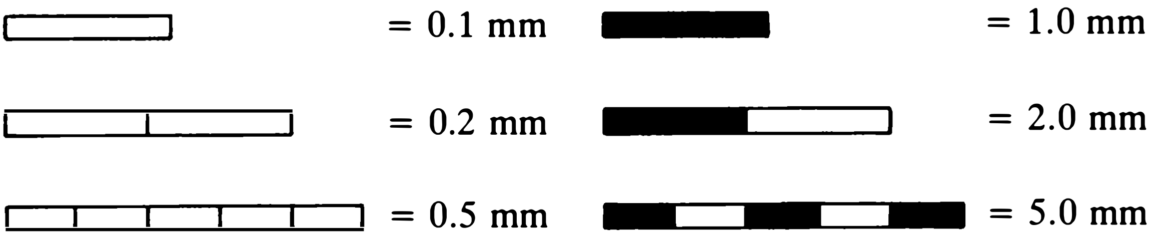
Diameters are given for the cylindrical species of *Chordeuma* and *Melogona*, and for all species of the order JULIDA; these are the *vertical* measures from dorsal to ventral poles (conveniently measured horizontally since the partly flexed animals usually rest laterally in the dish). The diameters given are therefore *heights* which are slightly larger than widths (more markedly so in *Chordeuma* and *Melogona*). See also note on p. 97.

Drawings and Scales

All the drawings are interpretive; stipple is used to indicate shape, by shadow from an upper left top-light, or to darken parts at a deeper focus. Some drawings attempt to depict actual appearance, using stipple to simulate colouration in addition to shape (e.g. Figs. 14A, 15B, 18A, 33D, E, 54A, B, 55A, 58B and 59A). The legends usually indicate the structure or appearance the drawings are designed to demonstrate; other contextual detail is not intended to be diagnostic. Thus, the setation of parts is frequently omitted, almost always, the setation of the legs is omitted, and even the legs themselves. For identification purposes, the drawings should therefore be used only in conjunction with the text.

Drawings were made directly from specimens, or parts thereof, lying in a dish of alcohol in their customary position of equilibrium. Where other views were necessary, position was maintained on a bed of glass beads. When higher magnification was necessary, drawings were made from parts mounted in lactic acid on a slide and covered with a coverslip. Drawings were made to scale by means of an eye-piece graticule of millimetre squares calibrated against a stage micrometer. The scale lines on the drawings are constructed using the following conventions:

Open rectangles used singly or together represent tenths of a millimetre. Black rectangles alone represent whole millimetres; longer scales in whole millimetres are represented by alternate black and open rectangles, as follows:



Classification

The recent publication of Hoffman's *Classification* (1979) and Demange's *Les Mille-pattes* (1981) has lead to inevitable changes from Schubart's *Tierwelt* (1934) and Brolemann's *Faune de France* (1935) which have stood for so long as ultimate authorities on the European fauna.

My ordinal nomenclature follows that of Hoffman but I have altered his arrangement of the helminthomorph orders and avoided using his groupings into superorders in order to maintain a relation with the older schemata. In doing this I am probably emphasising grades of organization which are so much easier to comprehend than conventional taxa. I have tried to keep in view my favourite (and heuristically helpful) scheme of Pentazonia, Trizonia and Monozonia used in my first edition. The three orders of the old Colobognatha are kept together to reflect that there are still some who consider them to be a natural group. Similarly, the three silk-spinning trizonian groups of the old Nematophora are kept together. Glomeridesmida and Polyzoniida are juxtaposed to indicate the affinity which Hoffman notes, as also are the Chordeumatida and the Platydesmida. Finally, the Spirobolida with their distinct pleurites are placed next to the trizonian orders.

I have followed Hoffman in grouping the chordeumatoids and the craspedosomatoids into the order Chordeumatida whilst noting that Demange chooses Craspedosomatida as his ordinal name and feeling that it might be better to allow ordinal status to each of these groups. My scheme for the British snake millipedes is a compromise between the simple grouping of thin and thick snakes into Blaniulidae and Julidae as in Hoffman's classification and according each ordinal status as Demange. I have accepted Enghoff's strong recommendation to separate the nemasomatids from the blaniulids but have resisted temptation to accord family status to the groups within the Julidae *s.l.* Within the restricted British fauna I think it is useful to underline the ecological and behavioural confamiliarity between *Ommatoiulus* and *Tachypodoiulus* and between *Julus, Ophyiulus* and *Leptoiulus*. I have accorded these groups mere tribal status bearing in mind the possible affinity of *Tachypodoiulus* and *Cylindroiulus* and the obvious structural differences between *Julus* and the other Julini *s.l.*

Scheme of Classification

Class DIPLOPODA		
Subclass PENICILLATA		
Order POLYXENIDA		
Subclass PENTAZONIA		
Order SPHAEROTHERIIDA*	Pentazonia	
Order GLOMERIDA		
Order GLOMERIDESMIDA*		
Subclass HELMINTHOMORPHA		
Order POLYZONIIDA		Colobognatha
Order SIPHONOPHORIDA*		
Order PLATYDESMIDA*	Trizonia	
Order CHORDEUMATIDA		Nematophora
Order STEMMIULIDA*		
Order CALLIPODIDA*		
Order SPIROBOLIDA*	Monozonia	Juliformia
Order SPIROSTREPTIDA*		
Order JULIDA		
Order POLYDESMIDA		

The Chordeumatida, Polydesmida and the three juliform orders account for 90% of all described species. In Britain, the orders Chordeumatida (9 species), Polydesmida (12 species) and Julida (26 species) account for 90% of the British species.

Orders marked with an asterisk are not represented in Britain.

Classification and List of Species

- Class DIPLOPODA
  - Subclass PENICILLATA
    - Order POLYXENIDA
      - Family Polyxenidae
        - *Polyxenus lagurus* (Linné)
  - Subclass PENTAZONIA
    - Order GLOMERIDA
      - Family Glomeridae
        - *Glomeris marginata* (Villers)
        - *Stygioglomeris crinata* Brolemann
        - (= *Geoglomeris jurassica* Verhoeff)
      - Family Trachysphaeridae
        - *Adenomeris gibbosa* Mauriès
  - Subclass HELMINTHOMORPHA
    - Order POLYZONIIDA
      - Family Polyzoniidae
        - *Polyzonium germanicum* Brandt
    - Order CHORDEUMATIDA
      - Suborder Craspedosomatidea
        - Family Craspedosomatidae
          - *Craspedosoma rawlinsii* Leach
          - *Nanogona polydesmoides* (Leach)
          - (= *Polymicrodon polydesmoides*)
        - Family Brachychaeteumatidae
          - *Brachychaeteuma melanops* Brade-Birks
          - *Brachychaeteuma bradeae* (Brolemann & Brade-Birks)
          - *Brachychaeteuma bagnalli* Verhoeff
      - Suborder Chordeumatidea
        - Family Chordeumatidae
          - *Chordeuma sylvestre* C. L. Koch
          - *Chordeuma proximum* Ribaut
          - *Melogona gallica* (Latzel)
          - (= *Microchordeuma gallicum*)
          - *Melogona scutellare* (Ribaut)
          - (= *Microchordeuma scutellare*)

- Order JULIDA
  - Family Nemasomatidae
    - *Thalassisobates littoralis* (Silvestri)
    - *Nemasoma varicorne* C. L. Koch
  - Family Blaniulidae
    - *Proteroiulus fuscus* (Am Stein)
    - *Choneiulus palmatus* (Nemec)
    - *Nopoiulus kochii* (Gervais)
    - *Blaniulus guttulatus* (Fabricius)
    - *Archiboreoiulus pallidus* (Brade-Birks)
    - *Boreoiulus tenuis* (Bigler)
  - Family Julidae
  - Tribe Schizophyllini
    - *Ommatoiulus sabulosus* (Linne)
    - *Tachypodoiulus niger* (Leach)
  - Tribe Cylindroiulini
    - *Cylindroiulus londinensis* (Leach)
    - *Cylindroiulus caeruleocinctus* (Wood)
    - *Cylindroiulus vulnerarius* (Berlese)
    - *Cylindroiulus nitidus* (Verhoeff)
    - *Cylindroiulus punctatus* (Leach)
    - *Cylindroiulus latestriatus* (Curtis)
    - *Cylindroiulus britannicus* (Verhoeff)
    - *Cylindroiulus parisiorum* (Brolemann & Verhoeff)
    - *Cylindroiulus truncorum* (Silvestri)
    - *Enantiulus armatus* (Ribaut)
  - Tribe Julini
    - *Julus scandinavius* Latzel
    - *Ophyiulus pilosus* (Newport)
    - *Leptoiulus belgicus* (Latzel)
    - *Leptoiulus kervillei* (Brolemann)
  - Tribe Metaiulini
    - *Metaiulus pratensis* Blower & Rolfe
  - Tribe Brachyiulini
    - *Brachyiulus pusillus* (Leach)
    - *Unciger foetidus* (C. L. Koch)

Order POLYDESMIDA
  Suborder Polydesmidea
    Family Haplodesmidae
      Prosopodesmus panporus Blower & Rundle
    Family Polydesmidae
      Polydesmus angustus Latzel
      Polydesmus testaceus C. L. Koch
      Polydesmus inconstans Latzel
      (= *P. coriaceus*)
      Polydesmus gallicus Latzel
      Polydesmus denticulatus C. L. Koch
      Brachydesmus superus Latzel
      Eumastigonodesmus boncii (Brolemann)
    Family Macrosternodesmidae
      Macrosternodesmus palicola Brolemann
      Ophiodesmus albonanus (Latzel)
  Suborder Paradoxosomatidea
    Family Paradoxosomatidae
      Oxidus gracilis (C. L. Koch)
      Stosatea italica (Latzel)

Notes on the List of Species: Changes from Blower (1958)

Additions

	Collector:	*Published:*
Adenomeris gibbosa Mauries	Doogue, 1979	this work
Chordeuma sylvestre C. L. Koch	Blower, 1963	Blower, 1974b
Chordeuma proximum Ribaut	Satchell, 1955	Nelson, 1964
Cylindroiulus truncorum (Silvestri)	Rundle, 1975	this work
C. vulnerarius (Berlese)	Rundle, 1975	this work
Enantiulus armatus (Ribaut)	Eason, 1958	Blower, 1974b
Prosopodesmus panporus Blower and Rundle	Rundle, 1975	Blower & Rundle, 1980
Unciger foetidus (C. L. Koch)	Jones, 1983	Jones (1985)

Cylindroiulus caeruleocinctus has been elevated to specific status; the old varietal name takes precedence over *C. iteutonicus* Pocock.

Name changes

Stygioglomeris crinata = Geoglomeris jurassica
Nanogona polydesmoides = Polymicrodon polydesmoides
Melogona scutellare = Microchordeuma scutellare
Melogona gallica = Microchordeuma gallicum
Nemasoma varicorne = Isobates varicornis
Thalassisobates littoralis = Isobates littoralis
Cylindroiulus caeruleocinctus = Cylindroiulus teutonicus
Ommatoiulus sabulosus = Schizophyllum sabulosum
Polydesmus inconstans = Polydesmus coriaceus (this name should now be given to *P. gallicus* but this change is deferred to avoid confusion)
Stosatea italica = Entothalassinum italicum

Change of authority

Blaniulus guttulatus (Fabricius) = *Blaniulus guttulatus* (Bosc)

Spelling

I have followed Dr. Jeekel's authority (Jeekel, 1971) in using the spelling *Julus*, Julidae, Julida etc. but retaining the root *-iulus* in compounds such as *Ophyiulus*, *Leptoiulus* etc.

Subgenera

Subgenera, which appeared in Blower (1958), are not included here.

Guide to identification

Thus, in the British fauna there are six orders with the following numbers of families, genera and species:

	Families	Genera	Species
POLYXENIDA	1	1	1
GLOMERIDA	2	3	3
POLYZONIIDA	1	1	1
CHORDEUMATIDA	3	5	9
JULIDA	3	17	26
POLYDESMIDA	4	8	12

In the first three orders there are (1) one species of bristly millipede, widespread but not often collected; (2) three species of pill millipedes, one large, brown-black and common, two others small, white and subterranean, and (3) *Polyzonium germanicum*, a rare species confined to the extreme south east of England. Reference to Figs. 14–18 will usually suffice to identify the British species in these first three orders.

The last three orders contain 47 of the 52 British species and reference to the keys must be made. Orders Julida and Polydesmida consist of the flat or round-backed moniliform, short-bodied (19 or 20 rings) polydesmidans and the smoothly cylindrical 'snake' millipedes or julidans, usually with more than 30 rings when adult. The order which may perplex beginners is the Chordeumatida; these are millipedes of medium length (28 or 30 rings when adult) which may be moniliform or even flat-backed, or smoothly cylindrical like the 'snakes'. It is therefore most important at the outset to recognize the ordinal characters of the Chordeumatida, principally the 3 + 3 setae on each ring and the undivided cheek lobes (Fig. 19).

Young stadia may be confused with adults of very small species – or *vice versa*; remember that young stadia have fewer rings than adults; the keys apply to all stadia as far as genera. Make sure you have referred your animal to the correct order before proceeding to family and species keys. Keep a special look-out for the small pallid species of *Brachychaeteuma* (p. 76) which have paranotal extensions to their rings and are difficult to see, and also the very small species of polydesmidans, *Eumastigonodesmus boncii* (p. 211), *Macrosternodesmus palicola* (p. 212) and *Ophiodesmus albonanus* (p. 214).

Systematic section

Key to the orders of British Diplopoda

1. Head, collum and tergites carrying two transverse rows of serrated hollow spines; a lateral tuft of similar spines on each pleurite except the first; two long brushes of spines terminally (Fig. 14). Adults with collum followed by nine tergites; thirteen pairs of legs .... POLYXENIDA (p. 52)

Without serrated spines on tergites and pleurites; setae on trunk, if present, simple. Tergites strongly arched, hiding ventrally placed pleurites and sternites (Fig. 3B, C) or with pleurites incorporated into a pleuro-tergal arch or three-quarter cylinder (Fig. 3D, E, F), or the sternites may be joined to the pleurotergal arch to give a completely cylindrical sclerite (Fig. 3A, G, H, I); pleurotergites with or without lateral or dorso-lateral expansions or paranota (Fig. 3) **2**

2. Tergal arches hemicylindrical, pleurites and sternites visible ventrally (Figs. 3B, C; 15–18) **3**

Pleuro-tergal arches three-quarter cylinders, with or without lateral or dorso-lateral expansions or paranota giving a sub-trapezoidal appearance (Fig. 3A, D–I) **4**

3. Twelve tergites, including telson (fewer in young stadia); second tergite (shield) much longer than the collum and following tergites; capable of enrolling into a sphere (Figs. 15–17) .... pill millipedes, GLOMERIDA (p. 56)

Adults with more than 30 tergites; pointed head (Fig. 18) rare species from South-east England .... POLYZONIIDA (p. 65)

4. Rings sub-trapezoidal, the metazonites produced laterally or dorso-laterally into lobed or keel-like paranota giving the appearance of a saddle-shaped or flat back (Fig. 3E–I) **5**

Rings cylindrical (Fig. 3A, D) **6**

5. Without ocelli. Adults with 19 or 20 rings (telson included). All females except stadium II with an odd number of pairs of legs. All males except stadium I with an even number of pairs of legs. Rings closed ventrally (Figs. 3G–I, 60, 67, 68) .... order POLYDESMIDA (p. 188)

With ocelli (except in stadium I); in adult *Brachychaeteuma* spp. there may be only three ill-defined ocelli. Adults with 30 rings (telson included); cheeks laterally protuberant, not obviously divided into cardines and stipetes; three pairs of setae on metazonites arranged as in Fig. 19. All stadia except I and II and male stadia VIII and IX with an even number of pairs of legs. Rings open ventrally (Fig. 3E, F) ....order CHORDEUMATIDA (p. 68)
..............................suborder CRASPEDOSOMATIDEA (p. 71)

6. Always with ocelli (except stadium I); collum not overlapping the head; cheeks laterally protuberant, not obviously divided into cardines and stipetes; no longitudinal striae or other sculpture on the ring; three pairs of setae on metazonites (Fig. 28). Adults with 28 or 30 rings (telson included), females with 45 or 49 pairs of legs, males with 41 or 45 pairs; all young stadia except I and II with an even number of pairs. Rings open ventrally. (Fig. 3D)
.... order CHORDEUMATIDA (p. 68)
.... suborder CHORDEUMATIDEA (p. 84)

With or without ocelli. Collum overlapping head. Cheeks not usually laterally protuberant and usually clearly divided into separate cardines and stipetes. Metazonites with longitudinal striae, grooves or fluting, at least ventrally. Posterior edge of metazonites with or without a whorl of fringing setae. Laterally placed ozopores on all rings from the sixth to the last podous. Adults usually with more than 30 rings*. All stadia with an odd number of pairs of legs. Rings closed ventrally. (Figs. 1, 3A, 32A) .... order JULIDA (p. 96)

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* *Nemasoma varicorne* (p. 102), *Proteroiulus fuscus* (p. 107) and *Brachyiulus pusillus* (p. 183) may mature with fewer than 30 rings (see p. 96).

Subclass PENICILLATA
Order POLYXENIDA

The bristly millipedes stand apart from all other millipedes in certain fundamental respects. The order Polyxenida is accordingly placed in a separate sub-class of the Diplopoda, the PENICILLATA (= PSELAPHOGNATHA) in antithesis to the remaining diplopods of the sub-class Chilognatha. The sclerites of bristly millipedes are not impregnated with calcium salts and do not form arched dorsal shields or coalesce into rigid units as in the chilognaths. The tergites and pleurites of the Polyxenida are armoured with characteristic serrated hollow setae or trichomes.

The genital openings are situated, as in all diplopods, on the third trunk unit behind the second pair of legs but there are no intromittent organs or gonopods. In contrast to all other diplopods, there is an indirect transfer of sperm between the sexes. Spermatophores are deposited by the males on to specially constructed webs and are later picked up by females guided to the spot by special directing threads. The whole process was described by Schömann (1956).

The gait of the Polyxenida is unique among diplopods; the propulsive legs all converge on to the same foothold in contrast to all other diplopoda where adjacent propulsive legs diverge from one another (Manton, 1956).

Details of their anamorphosis are given in Table 1. They hatch with three pairs of legs as most other diplopods; these correspond to the collum and tergites 2, 3 and 4. From stadium IV there is a single apodous unit behind the podous series, ready to become the single new podous unit in the next stadium. A pair of legs 'extra' to the diplopodous series appears to correspond to this partially embryonic unit but disappears in the adult (stadium VIII). According to Schömann (1956) adults in stadium VIII may moult again but without adding further segments and legs.

Only British species *Polyxenus lagurus* (p. 53).

Note: The old sub-class Chilognatha (all diplopods except bristly millipedes) was the equivalent of both the sub-classes PENTAZONIA and HELMINTHOMORPHA used in this *Synopsis*.

Polyxenus lagurus (Linné)
(Fig. 14)

Scolopendra lagura Linné, 1758: *Syst. Nat.*, ed. *10*: 637

Length: 2–3 mm   Breadth: 0.5–1.0 mm

Linneus classified the bristly millipede along with the centipede genera *Scolopendra, Lithobius* and *Scutigera* emphasizing how atypical it is as a diplopod, principally because of its dorsiventrally depressed strap-shaped body and its lack of calcification.

Light amber coloured but clothed in dark brown bristles or setae (**trichomes**). These trichomes are arranged in (a) two transverse rows united by lateral tufts on the head and each tergite including the collum; (b) in lateral tufts on each pleurite except the first, and (c) terminally as two long brushes borne on the telson.

The genital openings are situated behind the second pair of legs at the apex of truncated conical vulvae in the female and slightly longer pointed conical penes in the male (Fig. 14B, C). The species exhibits geographic parthenogenesis.

Vandel (1926) gave figures of declining percentages of males from Toulouse in southern France through the Netherlands, Denmark, Sweden, to Finland in the north; males were completely absent in this last country. Schömann (1956) and Meidell (1970) recognized two distinct forms, one sexual and the other parthenogenetic. Individuals of the sexual form have two median and two lateral red-brown lines on the dorsum which are absent from the parthenogenetic form; males are slightly smaller than females in the sexual form and their terminal trichome bundles are slimmer. The sexual forms appear to prefer humid coastal regions. Enghoff (1976b, 1978b) gives maps of the distribution of the two forms in Europe. Both forms appear in southern Scandinavia, the parthenogenetic form in mainland Germany, Poland and Russia and the sexual form in southern France and Holland.

Distribution

British Isles: Most often found under bark of dead trees, especially coniferous trees but also on the ground in leaf litter and under stones. There are several records of its occurrence in coastal regions at the roots of halophile plants such as sea pink and beneath lichens and moss cushions growing on boulders. It is an inhabitant of old stone or brick walls, in small colonies 'hanging on to the roof of extensive crevices which may be only just large enough for their entry, amidst an abundance of cast skins. *Polyxenus* presumably returns to the same roosting places after excursions in search of food.' (Manton, 1956). In the south it is occasionally seen walking on the exposed surface of old walls; Dr. Brade-Birks once took me to see (as no doubt many of his visitors) the animals out on the brick garden wall of his vicarage at Godmersham in Kent. I collected several individuals from this wall and subsequently found the collection to include both males and females. The sex of most of the animals in Britain has generally not been recorded but Fussey & Varndell (1980) have examined large samples from Bardsey Island and Anglesey in Wales and Saltwick Nab, near Whitby, North Yorkshire and report that the population at these three sites were largely, if not totally, bisexual.

There are widely scattered records in England and Wales (more from the south) and in Scotland (mainly southern) and from three eastern Irish counties (Antrim, Dublin and Wicklow).

Europe: The species is recorded throughout Europe. Also recorded from the Central Sahara at 2,810 m; U.S.A. (parthenogenetic form): Washington and New Jersey (Nguyen Duy-Jacquemin, 1976), Michigan (Eughoff, *pers. com.*) and Ohio (Kane, *pers. com.* to Enghoff).

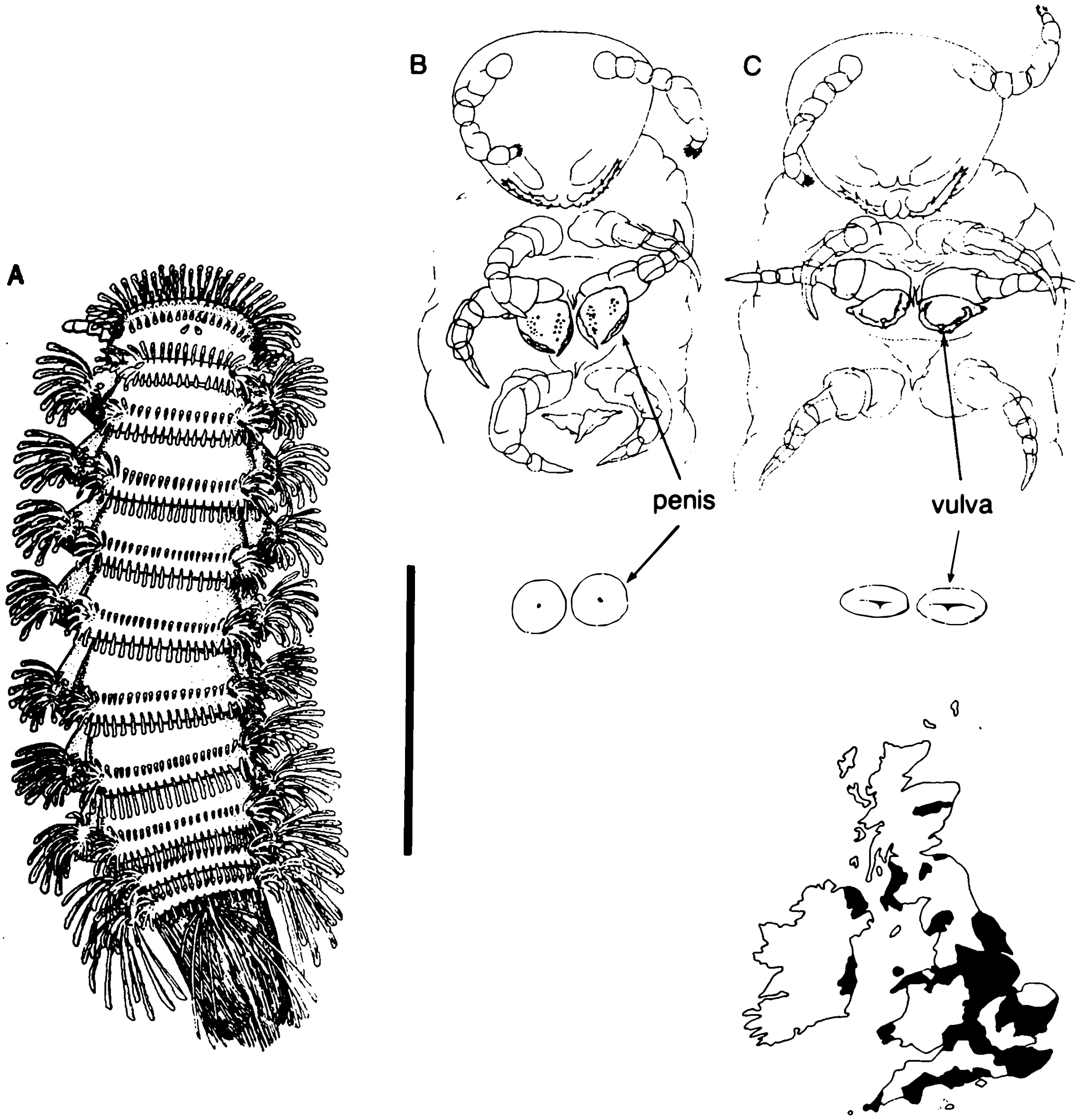


Fig. 14. *Polyxenus lagurus*. A. Dorsal view of whole animal; B. Ventral view of penes in the male; C. Ventral view of vulvae in the female. B & C from original drawings by Keith Hamer; apical views redrawn from Schömann (1956).

Subclass PENTAZONIA

Order GLOMERIDA

British species with twelve arched tergites, including the collum and the telson. Seventeen pairs of legs in the female, nineteen pairs in the male. The last three pairs of limbs in the male are modified as gonopods; the last pair are the largest and are called the telopods; because of this, an alternative name for the PENTAZONIA was OPISTHANDRIA; all other chilognaths have anteriorly placed gonopods (on ring VII) and were placed in the sub-class PROTERANDRIA, now called the HELMINTHOMORPHA. (See note on Chilognatha p. 52.

The sub-class name PENTAZONIA refers to the typical trunk unit consisting of five separately articulated sclerites; the tergal arches are almost half cylinders; paired pleurites and sternites are freely articulated within the concavity of the tergite (Fig. 3B). The first tergite or collum is small and has no pleural expansion; the second is a large **shield**; this last was originally believed to represent two fused tergites (the second and third) but its single nature was established by Dohle (1962). In the rolled-up position the head and collum are completely enclosed, the posterior edge of the telson abutting on to the anterior edge of the shield. The ventral edges of the succeeding tergites locate in ventro-lateral grooves on the shield (Fig. 15A). The shield transmits the thrust of the legs to the substrate as the animal pushes its way through the litter or soil; the shield is thus used in the same manner as the well-developed collum of the Julida.

The course of post-embryonic development is summarized in Table 1 for *Glomeris* and *Stygioglomeris*. The anamorphic phase of six or seven stadia is followed by a series of epimorphic stadia without addition of further legs and tergites. This type of development is called **hemianamorphosis**; it is only found in this order, the Polyxenida and in the exotic Spirobolida.

Bocock, Heath & Blower (1973) gave details for the anamorphosis of *Stygioglomeris* but made the mistake of assuming the number of anamorphic stadia to be the same as in *Glomeris*. Dohle (pers. com.) found a stadium of *Stygiolomeris jurassica* with six pairs of legs suggesting that this would be the second stadium and not the first as Bocock *et al.* (1973) suggested. Thus the first stadium with the full complement of legs is the sixth, not the fifth as is indicated in that paper. Also in contrast to *Glomeris*, the full complement of legs is not achieved until a stadium after that with 12 tergites – the seventh stadium.

Verhoeff described four stadia in *Glomeris* with the full complement of tergites and characterized these epimorphic stadia according to the degree of development of the telopods. Heath, Bocock & Mountford (1974) separated epimorphic stadia in *Glomeris marginata* using the discontinuous distribution of the fresh weights of individuals with twelve tergites; they proposed ten epimorphic stadia in males and eleven in females. Bocock *et al.* (1973)

found *Stygioglomeris crinata* carried mature eggs in what is now known to be stadium VII as did one individual in stadium VI (before anamorphosis was complete). By contrast, maturity in *Glomeris marginata* is not achieved until the second or third epimorphic stadia (males in stadium VII, females in stadium VIII). Details of the reproductive biology are known for *Glomeris marginata* and are briefly reviewed in the description of the species. No males of *S. crinata* have been found.

Key to British species of GLOMERIDA

1. Width of adult, or transverse diameter of pill, greater than 3.0 mm. Evenly black, brown or light brown with lighter edges to the tergites. No striae or grooves additional to the principal groove on ventral edge of shield. Eyes present (Fig. 15) .... *Glomeris marginata* (p. 58)

   Width of adult, or transverse diameter of pill, less than 2.0 mm. Without pigment, grey-white or cream-white. Shield with several grooves additional to the principal groove and sometimes with cuticular tubercles (Figs. 16, 17) **2**

2. Cuticle not clothed with cuticular tubercles; smooth except for two or three conspicuous striae or grooves on ventro-lateral lobes of tergites (Fig. 16) Females only .... *Stygioglomeris crinata* (p. 60)

   Cuticle clothed with cuticular tubercles, ideally (some tubercles may be rubbed-off) in two transverse rows on tergites and generally scattered over shield and telson (Fig 17). Males with telopods, and females, in roughly equal proportions .... *Adenomeris gibbosa* (p. 62)

Glomeris marginata (Villers)
(Fig. 15)

Oniscus marginatus Villers, 1789: *Caroli Linnaei Entomologica 4*: 187, pl. 11, Fig. 15

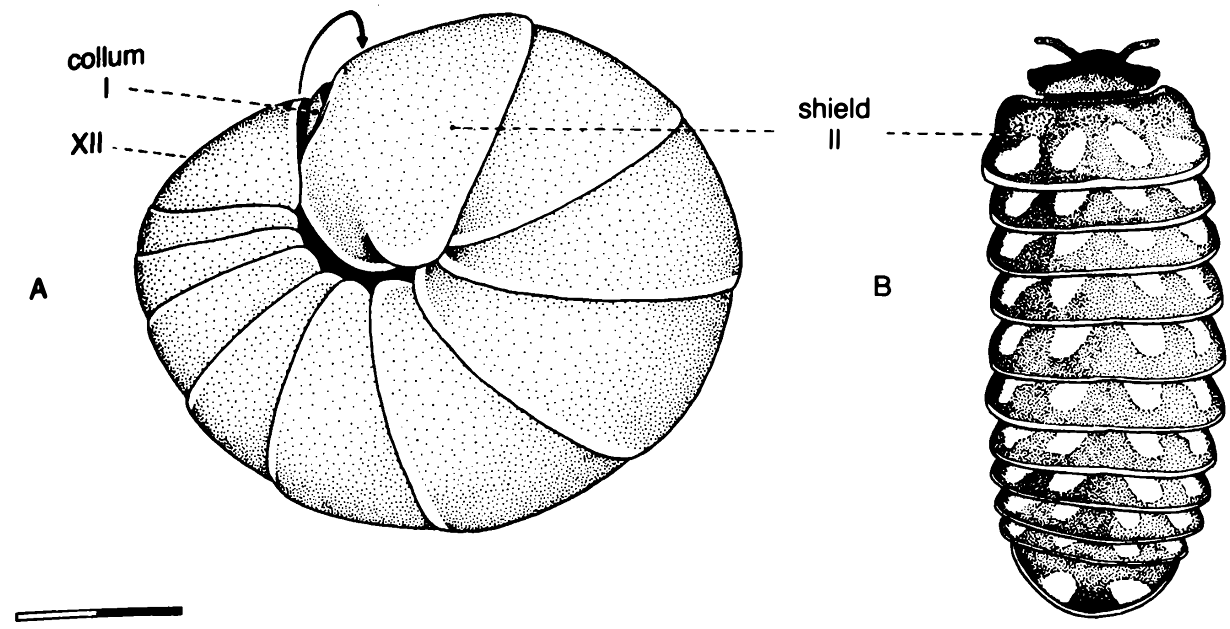
	Length:	Breadth:
Male	7–15 mm	3.5–6 mm (extended)
Female	8–20	4.0–8

Contracted (postmortem) length approximately twice the width; the fully enrolled 'pill' is oblate, the diameter in the vertical plane is slightly greater than that in the transverse plane, which latter is approximately equal to the width of the trunk. Typically brown or brown-black except the margins of the tergites but frequently straw coloured, brown and sometimes almost brick red. Anamorphic stadia with four light areas on each tergite and two on the telson (Fig. 15B) the so-called var. *perplexa*.

Biology. The pairing of the sexes has been described many times but only recently has the process of sperm transfer been fully understood (Haacker, 1964, 1969a). The male backs up to the female and grasps her vulvae with his telopods (Fig. 15C). At this stage the sperm has still to be transferred from the genital openings behind his second pair of legs to the telopods which are now in a position to insert it within the vulvae. Still grasping the vulvae, the male picks up a piece of soil or surface debris in his mandibles, fashions it into a smooth pellet and ejects a droplet of sperm on to the surface of the pellet. The pellet is then passed posteriorly leg by leg until it reaches the telopods. Slender processes of the telopods, the prefemoral styli (see Fig. 15C) position the pellet plus sperm droplet on the mesial coxal projections which then insert the sperm into the vulval openings. At the end of the process the pellet is abandoned having served its remarkable purpose.

Egg-laying females enclose their eggs, one by one in a capsule of soil passed through the gut and fashioned by the rectal walls. The capsules are superficially similar to over-sized faecal pellets. Adults collected in the spring readily produce an abundance of capsules in the collecting vessel. The course of post-embryonic development is shown in Table 1. Heath, Bocock & Mountford (1974) report that field populations in Cumbria proceed up to stadium IV in the first year; stadia II, III and IV overwinter and then develop into stadia V, VI and VII by the second winter and to stadia VII, VIII and IX by the third. Males are first mature at stadium VII (the second stadium with twelve tergites) and are therefore ready to breed in the second or third spring after their birth. Females do not mature until stadium VIII and therefore breed in their third or fourth spring. Adults moult just once per year in the autumn after reproduction and may proceed up to stadia XV or XVI at the age of ten or eleven years.

In an oak wood in Gower, South Wales, Blower & Miller (unpub.) had stadia III and IV in their winter samples, the majority being in stadium IV. In a Devon oak wood Blower & Gabbutt (1964) found that first year animals



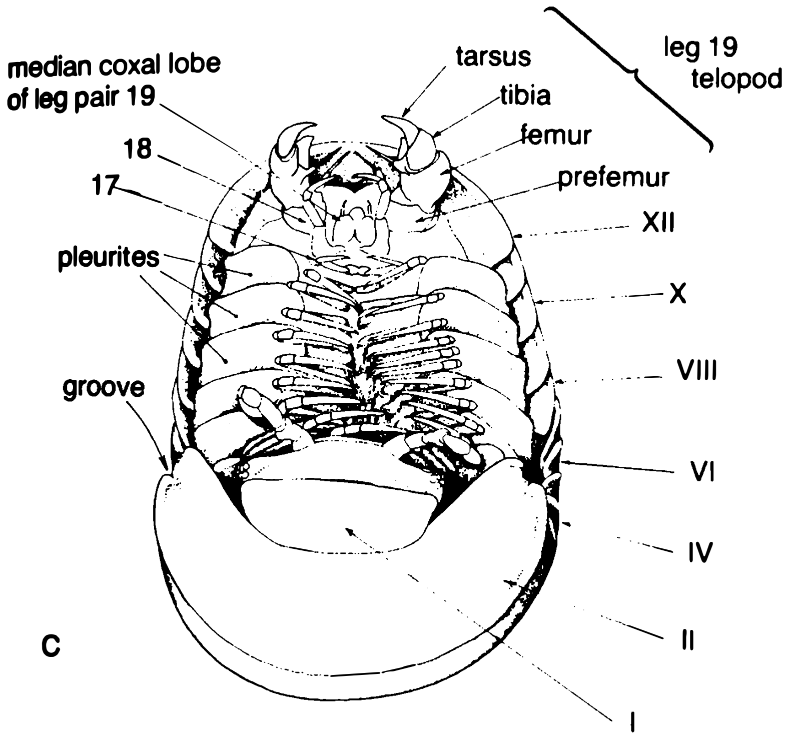


Fig. 15. *Glomeris marginata.* A. Partially enrolled animal to show the groove on the shield (ring II) which accommodates the ventral edges of the tergites; B. A juvenile showing the 'perplexa' markings usually confined to immature stadia; C. Ventral view of a partly flexed male to show the legs, separate pleurites, and the telopods (legs 19) used in pairing and insemination.

reached stadia IV and V with the emphasis on IV, by the first winter and none remained at stadium III. There is thus a slightly faster development in the south but data for the later years of growth are not available.

Like the long-lived iteroparous ommatoiulines, *Glomeris marginata* shows marked fluctuations in abundance at any one site; rarely does one come across a high density of one year old animals; even animals extracted by Tullgren funnels often show a bias towards the older age groups. Large numbers are often encountered in the most inhospitable places. For example, on the dunes and in the slacks around the Gower coast in autumn many dead and living animals may be picked up from the surface of the hot dry sand at mid-day.

Distribution

British Isles: Throughout England, Ireland and Wales and southern Scotland but not recorded north of the firths of Clyde and Forth except one record from Ross W. (VC 105), otherwise the most northerly records are from Renfrew, Stirling, Linlithgow and Edinburgh (map Fig. 15). Common in woodlands, except the most acid. It does inhabit poor sandy soils but is much more numerous in base rich loams. It can extend its range to non-wooded areas; Macfadyen (pers. com.) recorded very high densities in *Brachypodium* grassland in Whytham woods; even in farmland it may be found around the fields in hedge bottoms.

Europe: France, Switzerland, Germany, Austria and Czechoslovakia; Holland, Belgium, Denmark, Sweden (south of Lake Vanern), Norway only along the east coast. There is a distinct race in southern France and Spain.

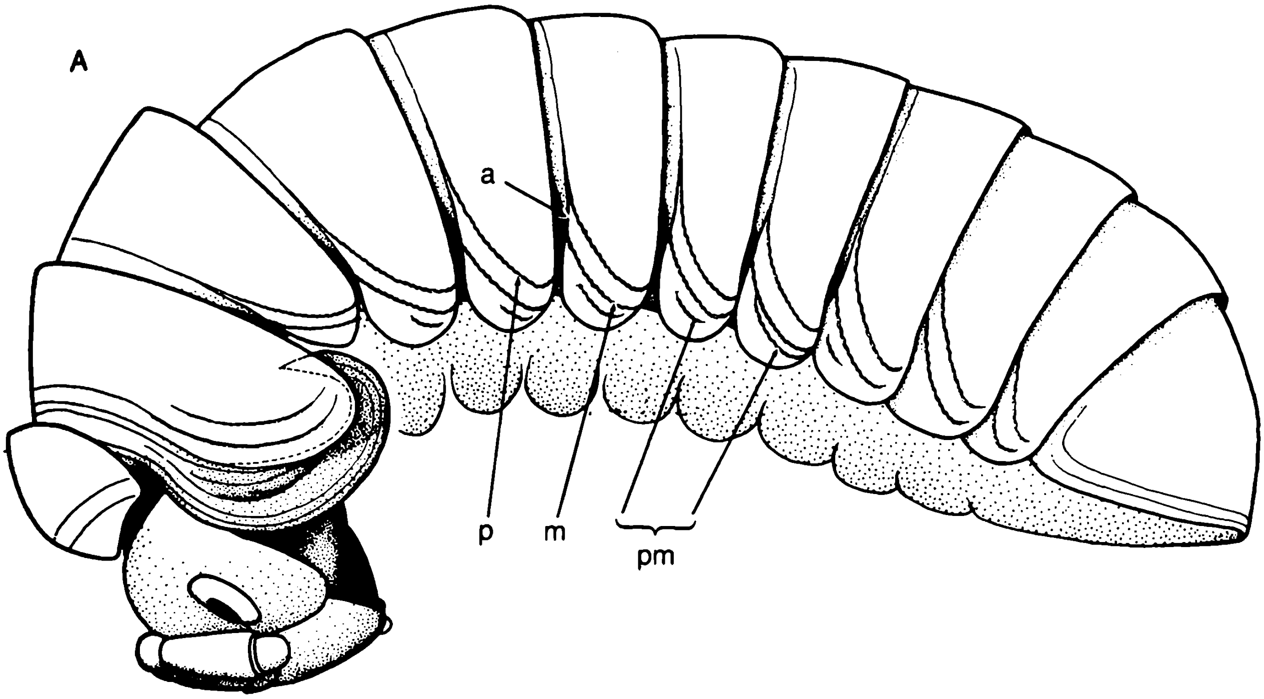
Stygioglomeris crinata Brolemann
(Fig. 16)

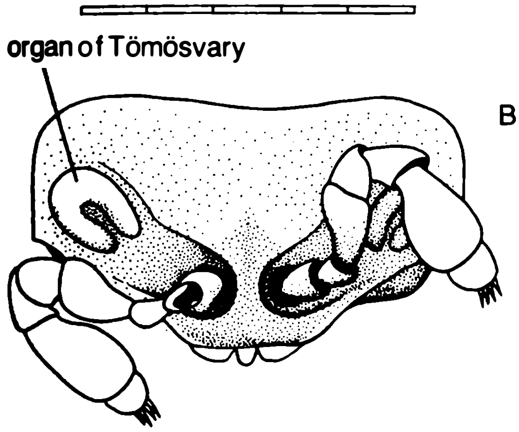
Stygioglomeris crinata Brolemann, 1913: *Arch. Zool. expér. gén. 52*: 387–445, pl. 15–19

Geoglomeris jurassica Verhoeff, 1915: *Zool. Anz. 46*: 21–24, Figs. 5, 8 and 9

Female stadium VII and beyond Length: 2.0–3.5 mm Breadth: 0.90–1.10 mm

A very small colourless glomerid with practically no pigment. Without ocelli. Head, collum, shield and tergites evenly clothed with microsetae but under the low power of a dissecting microscope the surface appears quite smooth and even. The anterior edge of the shield is produced into a definite lip; the anterior surface, against which the telson abuts in the enrolled position, is chased with several transverse grooves. The ventral notch, under which the ventral lobes of the tergites locate on enrollment is much more prominent than in *Glomeris*. These shield characters are very similar in *Adenomeris* but the rugose and sculptured tergites serve to distinguish the latter from *Stygioglomeris*. The antero-ventral portions of the tergite lobes are incised by characteristic obliquely running grooves (Fig. 16A); these are not so evident in *Adenomeris*.





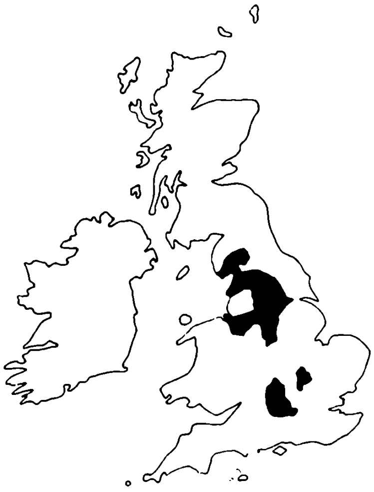


Fig. 16. *Stygioglomeris crinata.* A. Lateral view of a female (legs omitted). Note the postero-ventral groove on the shield (tergite II) which is more obvious than in *Glomeris* (Fig. 15A). The anterior (*a*), median (*m*), and paramedian (*pm*) grooves distinguish this small pale pill millipede from a close relative *S. subterranea*; B. Frontal view of head; note the conspicuous organ of Tömösvary. (From Blower, 1957.)

Biology. Bocock, Heath & Blower (1973) give some details of the biology of this species. No males of the species have been seen although nearly 500 individuals have been collected (mainly from Cumbria). The population in Cumbria probably reaches stadia III to V by the first winter and VI by the second. Eggs have been found in one individual at stadium VI but the majority of individuals mature at stadium VII.

Distribution

British Isles: First found in Whitham Woods, Berkshire by Dr. Overgaard Nielsen (Blower, 1957); later by Dr. Southern in Oxfordshire, 1966, Dr. Stephen Sutton near Wetherby in Yorkshire, 1968, near Grange over Sands, Cumbria (see Bocock *et al.* 1973) and more recently from Kerridge, Cheshire by Dr. Peter Miller and from Mill Dale in Derbyshire by myself. Most recently it has been found by Dr. Adrian Rundle from five sites in southern Bedfordshire, and from southwest Yorkshire (VC 63) and Mid Lancashire (VC 60).

Europe: Verhoeff (1915) described the species from the Jura district in Germany. In France it is recorded from the departments of Basses Alpes, Vaucluse and Ariège (in caves in the last two). *S. crinata* was found by Brolemann at the mouth of a cave in Ariège (1913) and later from a cave in Hautes Pyrénées (Demange 1965).

Adenomeris gibbosa Mauriès
(Fig. 17)

Adenomeris gibbosa Mauriès, 1960: *Bull. Soc. Hist. nat. Toulouse,* *95*: 401–404

Male	Length: 2.0–2.5 mm	Breadth: 0.8–1.0 mm
Female	2.5–3.2	0.9–1.1

Without ocelli. Females about the same size as those of *Stygioglomeris crinata* (p. 60) but immediately distinguishable by a clothing of typically cylindrical, sometimes distally expanded tubercles. These tubercles occur on the tergites in two rows, one along the tergite edge and another slightly anterior; these two rows give the impression of two transverse keels. The tubercles are more generally spread over the entire surface of the shield and the telson. The tubercles are amber to brown in colour and are unevenly developed; some individuals (as the extended animal in Fig. 17A) have lost (or not developed) their full complement of tubercles. The tubercles are not permanent structures but are hardened exudates from a group of fine pore canals passing through the cuticle. Their nature was first described in the related genus *Trachysphaera* (= *Gervaisia*).

Adenomeris gibbosa belongs to the family Trachysphaeridae, unlike *Glomeris marginata* (p. 58) and *Stygioglomeris crinata* (p. 60) which are members of the family Glomeridae.

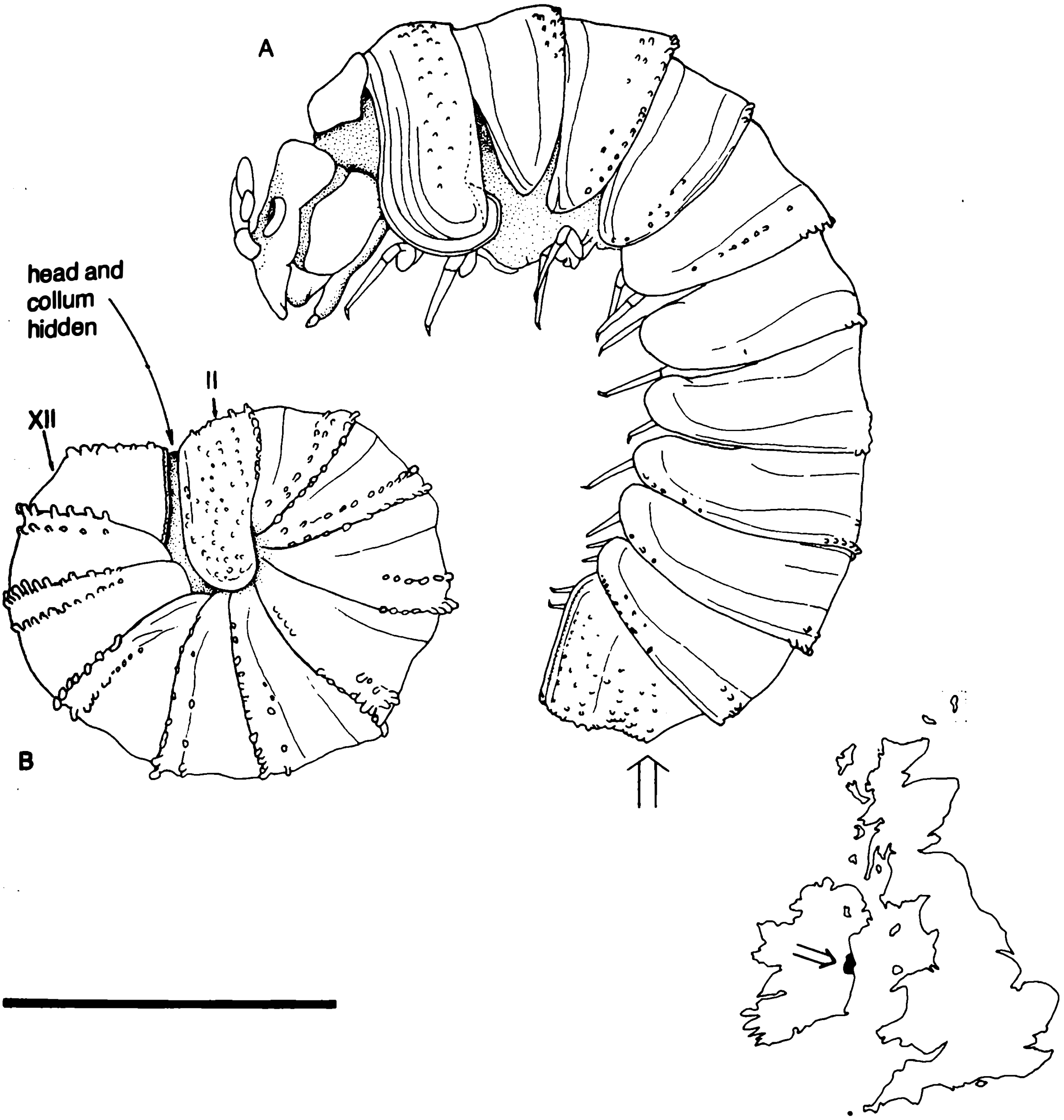


Fig. 17. *Adenomeris gibbosa.* A. Partly extended animal in lateral view; B. Enrolled individual. The ornamentation of the tergites is due to pillars of soft pliable material secreted through pore canals in the cuticle; these processes are easily rubbed off and it is rare to find an individual with a complete armature. The individual figured at B has a more complete set of tubercles than A.

Distribution

British Isles: First found by Mr. Delcan Doogue under a stone at the edge of a field (formerly a garden) at Ballygall, Dublin, Irish Republic. He found two females 18.11.78 and later five females closely associated with partially buried, partly decayed wood, 28.9.79. He also found both sexes in another locality near Dublin, under stones near an old house in cleared scrub on a limestone outcrop, 24.2.1981.

Europe: Ribaut (1909) based the genus on *A. hispida* from Eaux Bonnes (Basses-Pyrénées) and Sain Beat (Haute-Garonne). *A. gibbosa* differs from Ribaut's species in the presence of a median prominence on the telson. Mauriès found his species in the Hautes-Pyrénées in fallen calcareous debris concealed beneath moss and beech litter. Demange (1981) gives another record from Pyrénées-Atlantique.

Subclass HELMINTHOMORPHA

Order POLYZONIIDA

Hoffman (1979) gives separate ordinal status to this group which was originally placed, along with the Platydesmida and Siphonophorida, within the Colobognatha which had the status of a super order or even a sub-class. These three colobognath groups shared the reduced and highly modified mandibles and gnathochilarium (as the old name suggests), and leg-like gonopods with eight pairs of ambulatory legs in front of them. Hoffman considers this last feature as a primitive character retained by three otherwise unrelated groups. The platydesmidans have fairly normal mouth-parts; this, along with their trizonian condition, places them apart from the pentazonian polyzoniidans and siphonophoridans, which he considers as quite distinct in the manner and degree of modification of their mouth-parts.

Our British colobognath, *Polyzonium germanicum* (p. 66) belongs to the new order Polyzoniida. These are millipedes with primitive trunk design, pleurites and sternites are distinct and freely articulated with the tergal arches. They share their pentazonian condition with the Siphonophorida. The ninth and tenth pair of limbs are only slightly modified as gonopods. Unlike all other millipedes, the Polyzoniida (and the other two colobognath groups) hatch from the egg with four pairs of limbs as opposed to the usual three. It is better to view them as millipedes with an extra pair of limbs in front of the gonopods rather than having gonopods which have moved a segment further back. Another primitive character is the pair of eversible vesicles or coxal sac on each pair of limbs.

Polyzonium germanicum Brandt
(Fig. 18)

Polyzonium germanicum Brandt, 1831: *Bull. Mem. Acad. St. Petersb.* (6) *2*:2 1883, pl. XI

Male	Tergites incl. telson: 30–49	Length: 5.0–14.5 mm	Breadth: 1.1–1.9 mm
Female	38–55	5.0–17.5	1.2–2.4

Figures from Schubart (1934); the few British examples I have seen fall within the ranges given.

The pointed triangular head with 3 + 3 ocelli is almost invisible from above; it is directed ventrally and is shielded from view by the collum. Tergites yellowish to orange brown, pleurites lighter in colour. Brade-Birks (1920a) has drawn attention to the resemblance of enrolled animals to beech bud scales; Verhoeff compared them with dead needles of yew (*Taxus baccata*).

Distribution

British Isles: First discovered by Brade-Birks (1920a) in the litter of a juniper wood at Wye, east Kent. There are further records from Kent (a record from Surrey needs confirming). Recently Kime (1978) reports its absence from his survey area of Surrey, West Sussex and Hampshire and concludes the species is confined to the extreme south east.

Europe: According to Schubart (1934) the species occupies two distinct areas in Europe. The western area includes France and our own area in Kent and a northern and eastern area of south Sweden, Denmark, Latvia, Estonia and Finland; Germany north east of the Elbe, Poland, Czechoslovakia, Austria, Hungary, northern Yugoslavia, Albania, Romania, Bulgaria and USSR, European plain and Carpathians. It is notably absent from Norway, Holland, Belgium, mainland Denmark, West Germany, Switzerland and Italy.

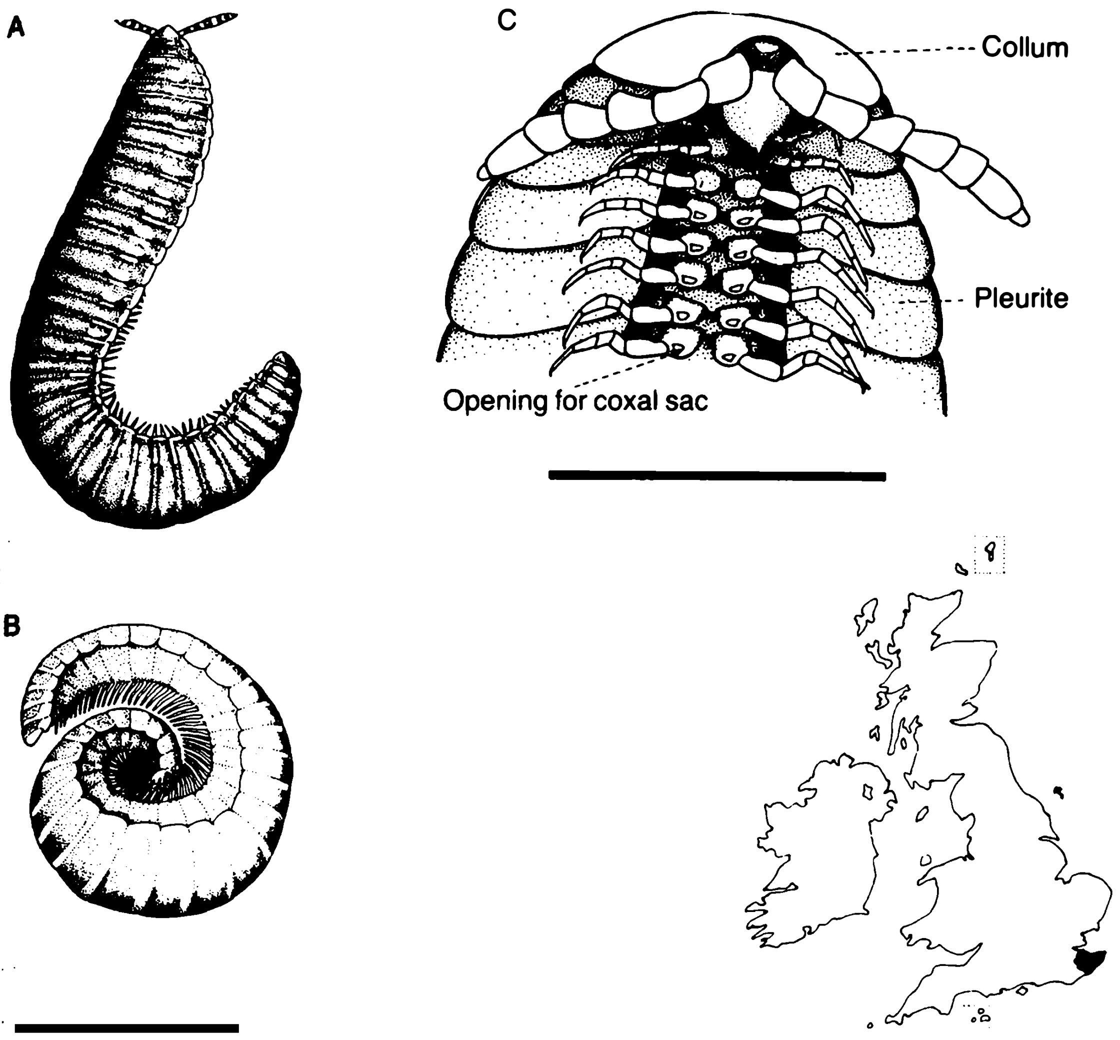


Fig. 18. *Polyzonium germanicum*. A. A sketch of the extended animal and B, an enrolled individual, drawn from photographs by Dr. S. M. Manton; C. Ventral view to show the ventrally curved head, triangular in outline, with three ocelli each side, and the legs with the openings for the coxal sacs. Note that the sternites and pleurites are separate entities.

Subclass HELMINTHOMORPHA

Order CHORDEUMATIDA

(= Order NEMATOPHORA of Blower (1958))

Always with ocelli; in Craspedosomatidae and *Chordeuma* they form an equilateral triangle (Figs. 19–21, 25C); in *Melogona* they form a more acute angled triangle with rarely more than four ocelli per row (Fig. 25A, B); in *Brachychaeteuma* they form a single antero-posterior line of three or six ocelli (Fig. 22). The ocular field grows by addition of a row of ocelli in front of the existing group at each moult. In Chordeumatida, unlike the condition in Julida, only one ocellus is added in each of stadia II and III (Figs. 10, 11, 19–21 and 25). Cheeks (basal mandibular lobes) laterally expanded and very prominent, not obviously divided into separate cardines and stipetes; a groove on the cephalic (dorsal) face indicates the division but is only discernible with difficulty. The collum does not overlap the head. Rings cylindrical or produced dorso-laterally into lobed or keel-like paranota (those of *Brachychaeteuma* are not very evident). Rings open ventrally (Figs. 3D, E, F and 19); the sternites are displaceable in relation to the pleuro-tergal arch; the ventral edges of the pleuro-tergal arches are visible laterally. All species have three pairs of setae on each ring, anteromedians, anterolaterals and postero-laterals; the laterals occur on anterior and posterior faces of the paranota, where these occur. As the old ordinal name Nematophora implies, these millipedes are the 'carriers of thread'; a pair of spinnerets protrude from under the dorsal part of the pre-anal ring (Figs. 20 and 28). Silk is used by the female to weave the nest and by both sexes to weave the moulting chambers. The hindermost pairs of legs are positioned more posteriorly than in other millipedes in order to manipulate the silk. There are no ozadenes in this order of millipedes.

There are nine stadia with 6, 8, 11, 15, 19, 23, 26, 28 and 30 rings, telson included (except in *Melogona scutellare* which matures at stadium VIII with 28 rings). The first and second stadia have three and five pairs of legs respectively, all other stadia have an even number of pairs except adults of *Chordeuma* and *Melogona* (see Table 1). In the Craspedosomatidea the 8th pair of limbs is modified as gonopods and the 9th as paragonopods. In the Chordeumatidae, the 8th limbs are peltogonopods and the 9th form the gonopods proper but, in addition, the posterior pair of limbs on ring VI (7th pair) and both pairs on ring VIII (pairs 10 and 11) are incorporated into the gonopodal apparatus (p. 84).

Chordeumatida are winter active; they oviposit in winter or early spring. Nests of *Nanogona polydesmoides* (p. 74) have been found as early as November. Most of the British species appear to be annuals.

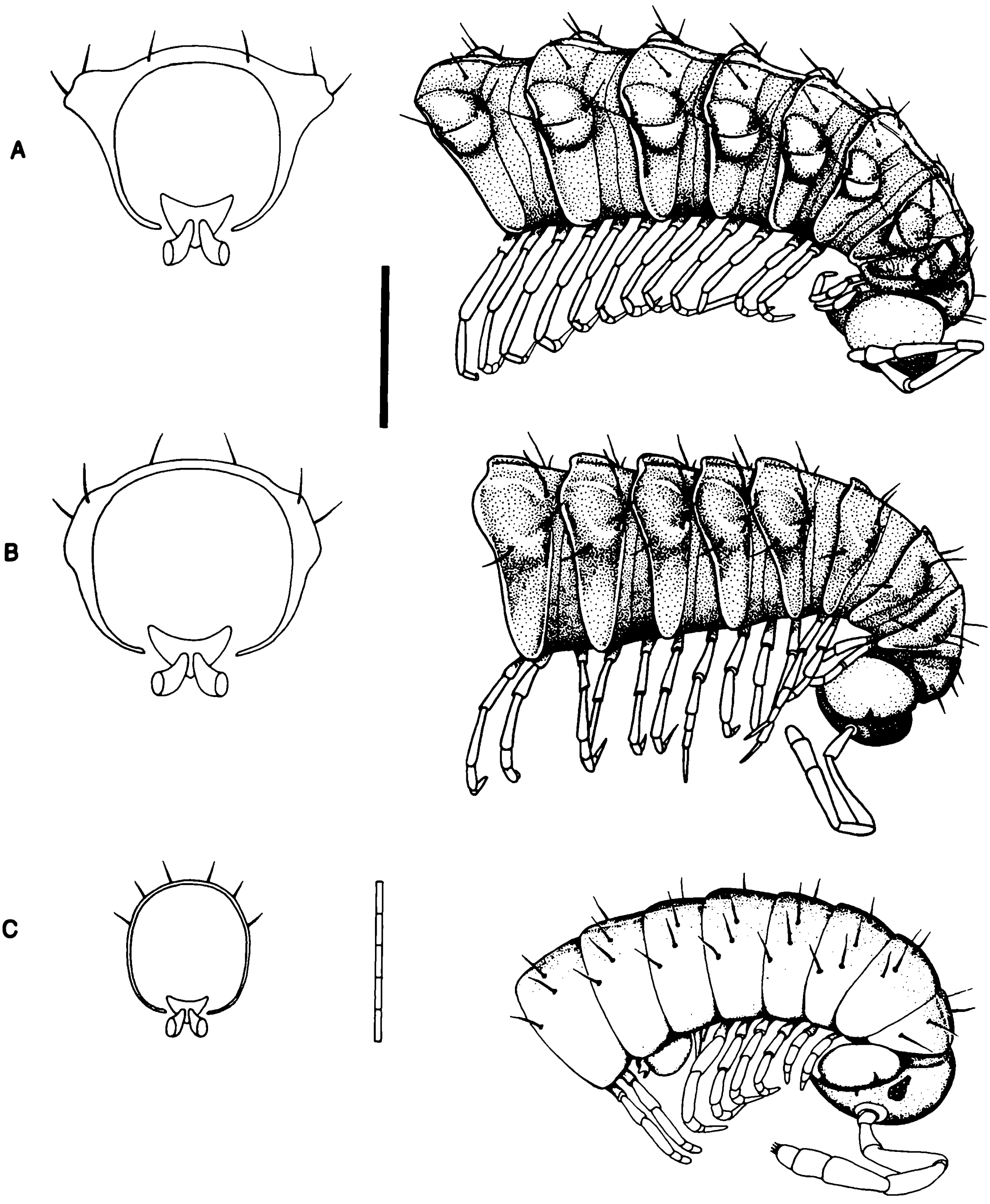


Fig. 19. The Order CHORDEUMATIDA. General views of the head ends and cross sections to show the range of architecture of the pleurotergal arches. Suborder Craspedosomatidea. A. *Nanogona polydesmoides* with keel-like paranota; B. *craspedosoma rawlinsii* with rounded, lobe-like paranota; Suborder Chordeumatidea; C. *Melogona scutellare* with smooth sub-cylindrical pleurotergal arches without paranota. Note the almost completely undivided cheek lobes (cardo and stipes all one piece), and the three setae on each side of the tergites, the ventral pair lying closer to the posterior edge; undivided cheeks and three pairs of setae are characters of the order.

Key to British families of CHORDEUMATIDA

1. Rings smoothly cylindrical (animals superficially juliform). One of the four species matures at stadium VIII with 28 rings (telson included), the other three mature at stadium IX with 30 rings (telson included). (Figs. 19c, 28a) .... suborder CHORDEUMATIDEA, ... family CHORDEUMATIDAE (p. 84)

Rings expanded dorsolaterally into keel-like or rounded lobes (paranota); the lobes are not very obvious in the small pale species of *Brachychaeteuma*. All with 30 rings in the adults (Figs. 20, 21 and 22) .... suborder CRASPEDOSOMATIDEA **2**

2. Larger, adults greater than 15 mm long and 1.2 mm broad. Well-pigmented species with polydesmid-like paranota or rounded lobes. Ocelli in a triangular field (Figs. 20 and 21) .... family CRASPEDOSOMATIDAE (p. 71)

Smaller, adults less than 8.5 mm long and 0.7 mm broad. Very weakly pigmented with inconspicuous paranotal lobes. Ocelli not very evident; adults with a single irregular antero-posterior row of six ocelli in one species or three ocelli in the other two (Fig. 22) .... family BRACHYCHAETEUMATIDAE (p. 76)

Suborder CRASPEDOSOMATIDEA

This suborder is represented in Britain by two larger species of the family Craspedosomatidae and three much smaller species in the family Brachychaeteumidae. The subordinal name means literally 'edge-bodied', the 'edges' being the often keel-like paranota. In one of our craspedosomatids, *Nanogona polydesmoides* the paranota are indeed keel-like, but in the other, *Craspedosoma rawlinsii* and in the three species of Brachychaeteumidae, they are more rounded lobes. The arrangement of gonopods is the reverse of that in the Julida and in the other suborder of the Chordeumatida, the Chordeumatidea, the modified limbs of the 8th pair are the gonopods proper, those of the 9th pair are paragonopods.

Family CRASPEDOSOMATIDAE

Ocelli well developed forming a more or less equilateral triangle; paranota always present, aliform and horizontal in *Nanogona*, rounded and lobe-like in *Craspedosoma* (the two genera represented in Britain belong to separate subfamilies). The anterior pair of limbs on ring VII (8th pair) are the gonopods proper and consist of lateral telopodites, the cheirites ('hands'), in between which a coxal piece is found and this is clothed either side by comb-like tines in *Nanogona*. The posterior pair of limbs (pair 9) are the paragonopods and consist of a broad sternal base from which six processes arise – the 'podosternite'. The detailed shapes and sizes of the podosternal processes may be very variable and is the reason for numerous subspecies and varieties of *C. rawlinsii* on the continent.

Key to the British species of Craspedosomatidae

1. With dorsolateral keel-like paranota giving a polydesmid appearance. Evenly coloured, light brown (Fig. 21) .... *Nanogona polydesmoides* (p. 74)

   With dorsolateral lobiform paranota giving a rounded trapezoidal cross-section. Darker and more varied in colour than *N. polydesmoides* (Fig. 20) .... *Craspedosoma rawlinsii* (p. 72)

Craspedosoma rawlinsii Leach
(Fig. 20)

Craspedosoma Rawlinsi Leach, 1815: *Trans. Linn. Soc. Lond., 11*, 380
C. simile Verhoeff, 1910

Adult Length: 15–16 mm **Breadth:** 1.2–1.7 mm

A handsomely coloured animal. A deep rich reddish brown pigment lies in narrow dorsal bands on either side of the median dorsal dark line, internal to the median setae and in lateral bands below the paranota, below the dorso-lateral and lateral setae; a narrow swathe connects these bands and there are invading peninsulas around the dorsal edge of the paranota. Light amber areas are left around the dorso-median setae and over most of the paranota. The paranota are smoothly rounded lobes quite distinct from the dorso-lateral keels of *Nanogona*.

Biology. Information on young stadia is not available. Most of the records are of adults collected in the winter months.

Distribution

British Isles: First recorded by Leach (1815). Quite a rare animal in England, usually found in woods, in moist places in litter, under stones or bark. Often close to a watercourse or in an area of natural drainage where moisture is assured at most seasons. It is apparently less dependent on base status than *Nanogona* and occurs in quite acid woods on sandy soil. The species has been recorded more frequently in the North; it is ranked fourteenth and sixteenth respectively in order of commonness in Scotland and Ireland, but twenty-fifth in England. It is interesting to note the number of Scottish records which come from flood refuse bordering lakes and rivers.

Europe: France (Allier possibly also in the North), Belgium, Holland, Denmark, southern Norway and Sweden, and Germany. Elsewhere in Europe this species is replaced by close relatives of the same genus. Brolemann (1935) regards these different European species as probably races of one very large and variable species with *C. rawlinsii* as the northern and western representative. However, each form of this European species has received specific status and each of these have been divided into numerous sub-species, and these into many forms of lower status.

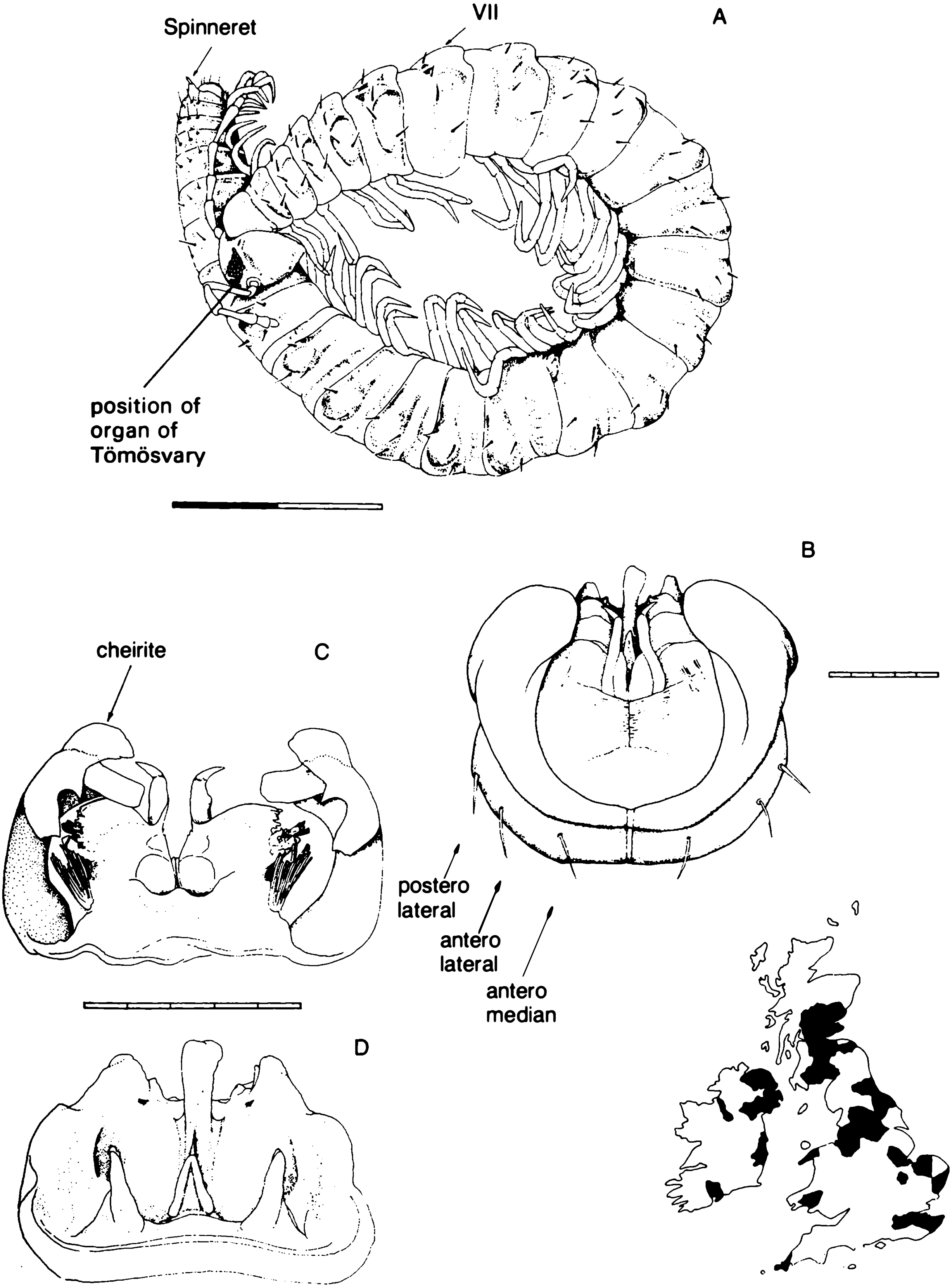


Fig. 20. *Craspedosoma rawlinsii.* A. Adult male, anteriorly in dorso-lateral view, passing into slightly ventrolateral view by ring XVI. Slight damage between rings XVI and XVII leads to the posterior rings lying in an exactly lateral view. The animal is a mature male in stadium IX, with eight rows of ocelli (only a single ocellus in rows 1 and 2. Note the organ of Tömösvary at the anterior apex of the ocular triangle); B. Ring VII viewed from in front with gonopods and paragonopods in position; C. Gonopods, the anterior modified limbs (8) of ring VII, in posterior view; D. Paragonopods, the posterior modified limbs (9) of ring VII, in anterior view.

Nanogona polydesmoides (Leach)
(Fig. 21)

Craspedosoma polydesmoides Leach, 1815: *Trans. Linn. Soc. Lond.* *11* (2): 380
Polymicrodon polydesmoides of Blower (1958) and all authors previous to 1980

Adult **Length:** 17–21 mm **Breadth:** 2.0–2.5 mm

Evenly coloured fawn to dark brown. The paranota are distinct dorso-lateral keels and the whole appearance reminiscent of the flat-backed *Polydesmus*, hence the trivial name. However, the dorsum and paranota are quite smooth; and the distinctive 3 + 3 setae and the complement of thirty tergites are quite characteristic. The 3 + 3 setae on each ring are noticeably much longer in the younger stadia.

Biology. Although this is the largest and commonest of our Chordeumatida the species has never been studied as a population; but detailed analysis of field records provides the following notes. Like our other nematophorans, the species is demonstrably winter active. Adults of both sexes have been observed moving about quite rapidly in the most superficial layer of frozen litter on New Year's Day. The silken tent-shaped nests have been seen in November and December. Stadia II and III occur in February along with adults. Stadium IV occurs in March and April, V and VI in April, VI right through to July. Stadium VII has been found in June, July and August, VIII in July, August and September and adults (stadium IX) in all months except May and June. In a Cheshire wood, adults fell into pitfalls from September to March.

There appears therefore to be an annual cycle with a fairly long period of egg-laying, probably from November to January since nests have been seen in November and stadium II as late as late February. The occurrence of adults as early as July may indicate that they might pass May and June in unnoticed aestivation and survive for a further season. However, there is a marked preponderance of sub-adult stadia (VIII) in September suggesting that this is the average achievement of that year's generation.

Distribution

British Isles: First recorded by Leach (1815). Typically found under stones, fallen logs, bark, especially in or near woodland but also in open land by the coast, in quarries but rarely in or around arable fields. More common in limestone districts but not confined to these. It is the commonest millipede recorded from British caves.

It occurs throughout Britain and Ireland where it is the fifth most frequently recorded millipede but in the south central and south eastern counties of England it is less frequent (Kime, 1978) and falls in rank to tenth place in his list. Kime associates it in the south and east with calcareous soils

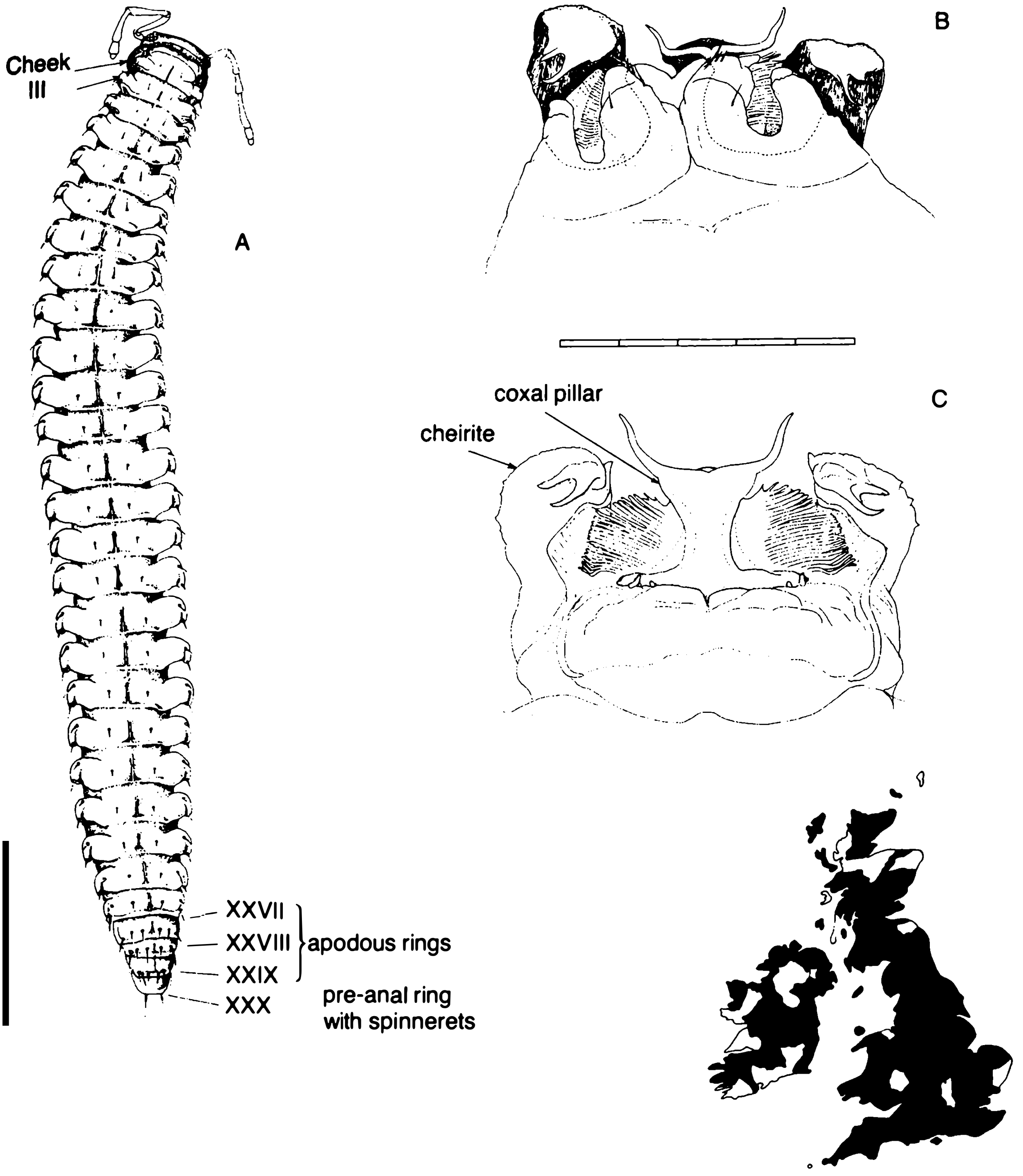


Fig. 21. *Nanogona polydesmoides*. A. Dorsal view of an adult female showing the superficial resemblance of the flat back to that of *Polydesmus* (compare, for example, Fig. 64A), hence the trivial name *polydesmoides*; B. Posterior view of the paragonopods and the gonopods behind (modified limbs 8 and 9); C. The same preparations as in B with the paragonopods removed revealing the anterior face of the gonopods.

especially in escarpment beech woods but remarks that it is much commoner in the west.

Europe: Widely distributed throughout France, most often in caves, subterranean quarries and mines but also epigeic. Elsewhere only as an isolated race *italicum* Manfredi, from the alps and a cave in northern Italy.

Family BRACHYCHAETEUMIDAE

Originally a British (and initially northern English) family with a single genus and three species, all of which were first described from Britain. Richard Bagnall found a single male from Durham for which Verhoeff (1911–1912) erected a new species, genus and family (*Brachychaeteuma bagnalli*). Six years later, Brade-Birks found a species near to his home at Darwen in Lancashire which was confamilial with *B. bagnalli* for which Brolemann and Brade-Birks erected a new genus and species (Brade-Birks 1917c) *Iacksoneuma bradeae* in honour of Dr. Randall Jackson. Later, Brade-Birks (1918a) re-examined the types of *B. bagnalli* and found Verhoeff's description to be faulty, principally in his assertion that *B. bagnalli* was blind and had no definite paranotal expansions. Since *bagnalli* did have eyes and paranota, Brade-Birks decided that *Iacksoneuma bradeae* and *B. bagnalli* were congeneric, *Brachychaeteuma* taking precedence. Finally, Bagnall found a third species in Dorset which had slightly more obvious ocelli; this was *B. melanops* Brade-Birks, 1918b. The moral of this story is that the ocelli (at least in *bradeae* and *bagnalli*) are very difficult to see, as are the paranotal expansions, and that small whitish diplopods must be examined very carefully. Furthermore, species of *Brachychaeteuma* occur associated with other small poorly pigmented species such as the chordeumatid *Melogona scutellare* (p. 94), two very small pigmentless polydesmidans, *Macrosternodesmus palicola* (p. 212) and *Ophiodesmus albonanus* (p. 214), and the blind blaniulids, *Boreoiulus tenuis* (p. 120) and *Blaniulus guttulats* (p. 116) from which they are by no means easy to distinguish in the field.

Small pale species with few ocelli, six in *Brachychaeteuma melanops*, but only three ill-defined in *bradeae* and *bagnalli*, arranged in a single antero-posterior series (Fig. 22). The paranota are lobe-like but rather indistinct. As in the Craspedosomatidae the gonopods proper are derived from the limbs of the 8th pair, and the 9th pair form paragonopods. The gonopods differ from those of the Craspedosomatidae, in that the telopodites are only represented by sinuous flagelliform processes; the remainder of the organ is coxal in origin and consists of a basin-shaped base produced into anterior and posterior processes (the syncolpocoxite of Brolemann, 1935). It is the anterior pair of processes from this **syncolpocoxite** which enables us to separate *bagnalli* from *bradeae* which are externally indistinguishable. The original species of the family (*B. bagnalli*) occurs in caves in Belgium and N.W. Germany. *B. bradeae* has been found rarely in France, Germany and Sweden, and *B. melanops* has been found more widely in France. Since Brolemann (1935) and Schubart (1934), six further species of the genus and family have been described from localities in the southern half of France, four of them from caves.

Key to the adults of the British species of Brachychaeteumatidae

1. With 4–6 well pigmented ocelli in a single, irregular antero-posterior line. Gonopods as in Fig. 22 .... *Brachychaeteuma melanops* (p. 78)

With three ill-defined ocelli in a single antero-posterior line **2**

2. Gonopods as in Fig. 24 .... *Brachychaeteuma bagnalli* (p. 82)

Gonopods as in Fig. 23 .... *Brachychaeteuma bradeae* (p. 80)

Brachychaeteuma melanops Brade-Birks
(Fig. 22)

Brachychaeteuma melanops Brade-Birks, 1918: *J. Zool. Res.*, *3*: 55–61, Figs. 1–6

Adult Length: 7.5 mm Breadth: 0.70 mm

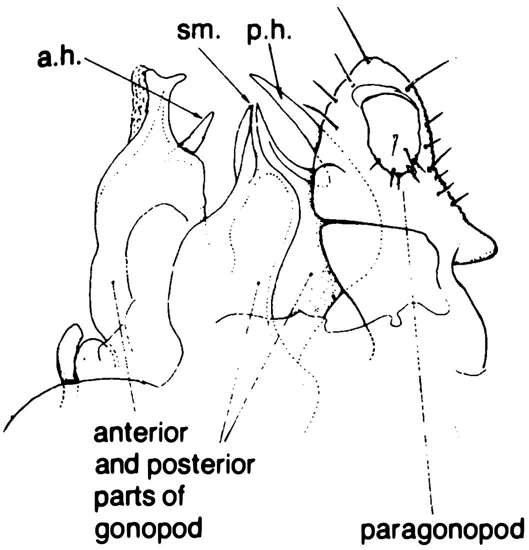
Up to six ocelli, the higher number in a single antero-posterior line of four and an extra two above. Anterior lobes of gonopods with a posteriorly directed horizontal process. Posterior horns noticeably higher (more distal) than in *bagnalli* and *bradeae*.

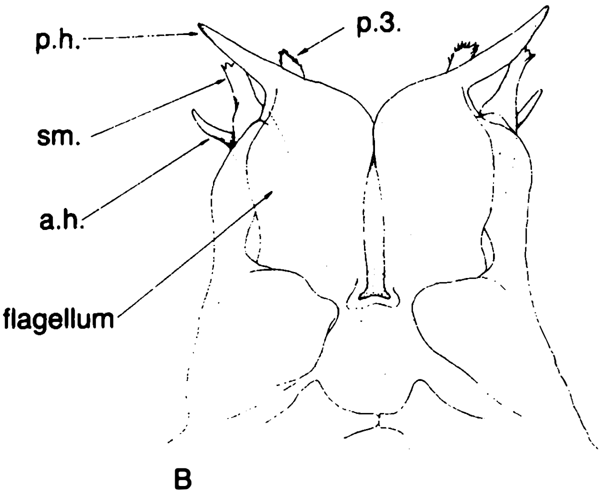
Distribution

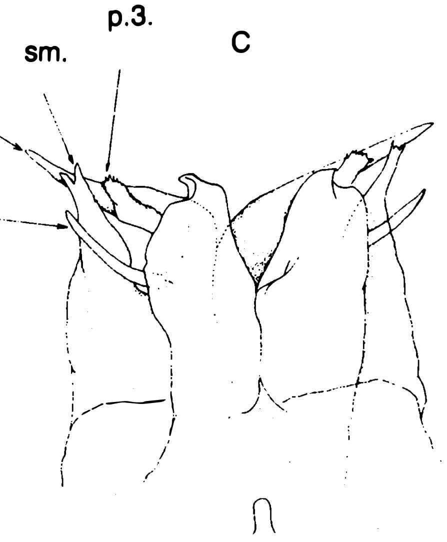
British Isles: First found by Bagnall at Swanage in Dorset in April 1918 and described by Brade-Birks (1918b) as new to science. The second records came from Devon, near Torquay and Babbacombe and were also due to Bagnall (1919). Thirdly a single male was found in 1943 by Turk (1944) at Polbathic, East Cornwall and I had a single male in Rocky Valley by Tintagel in North Cornwall in April 1963; this last was found in association with *Ophiodesmus albonanus*. Dr. J. L. Harding found a male in a garden in West West Kent in March 1967. The species was found in three separate kilometer squares in Surrey and one in Sussex, all in chalk or basic soils (Kime, 1978). Most recently it has been recorded from Otter Hole cave near Chepstow in Monmouthshire (Chapman, 1979).

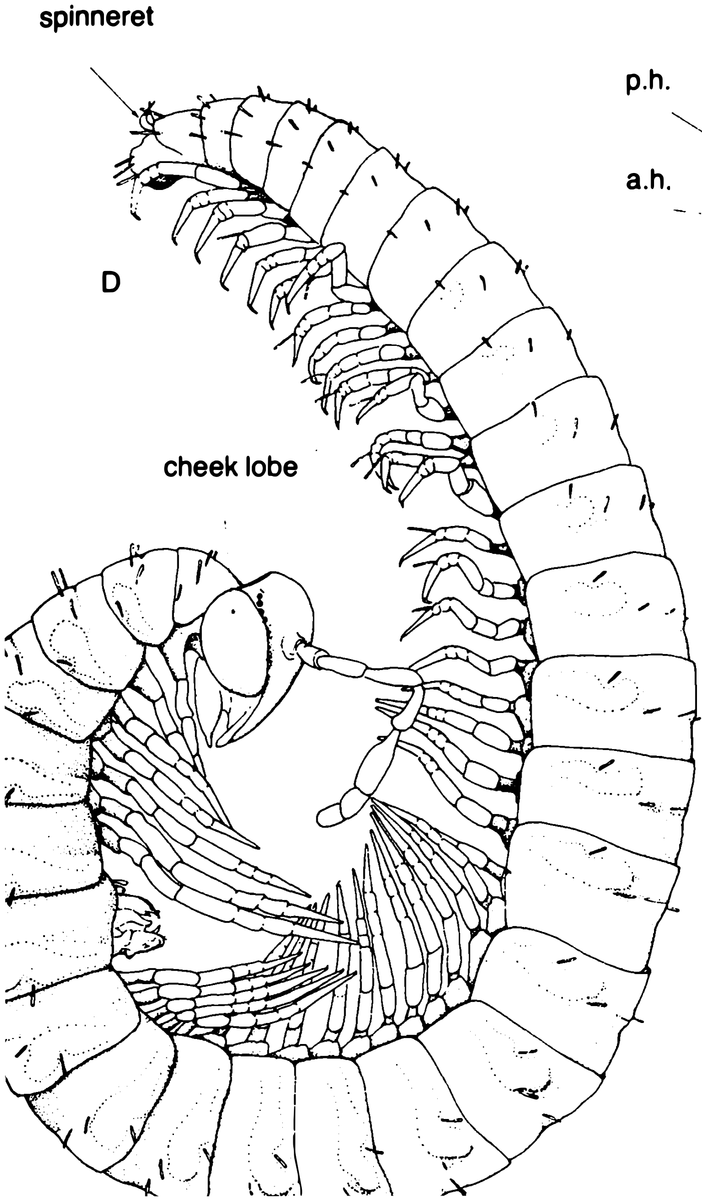
Europe: The earliest record outside Britain is that of Brolemann (1935) near to his home in Pau, Basses Pyrénées. His male differed slightly from the type and he erected the subspecies *horticola* to receive it. The animal from Polbathic in Cornwall had gonopods approaching this sub-species (Turk, 1944). Demange (1981) records it from six further French Departments in the north, west and south.

Fig. 22. *Brachychaeteuma melanops*. A. Lateral view of gonopods and paragonopods from the right hand side; B. Posterior view of the gonopods; C. Anterior view of the gonopods; D. Lateral view of a mature male; note the rounded paranota; these are similar to those of *Craspedosoma* (Fig. 20) but are not nearly so evident, partly due to the lack of pigment; note also the laterally protuberant cheek, not divided into separate cardo and stipes. *ah* anterior horn of gonopod; *ph* posterior horn of gonopod, *p.3* third process of gonopod; *sm* solenomerite.


a.h.
sm.
p.h.
anterior and posterior parts of gonopod
paragonopod


p.h.
p.3.
sm.
a.h.
flagellum
B


p.3.
sm.
C
p.h.
a.h.


spinneret
D
cheek lobe

Brachychaeteuma bradeae (Brolemann & Brade-Birks)
(Fig. 23)

Iacksoneuma bradeae Brolemann & Brade-Birks, 1917 *in* Brade-Birks,
H. K. & S. G. (1917c): *J. Zool. Res.*, *2*: 138–148,
Figs. 1–21

Male	Length: 5.5–8.0 mm	Breadth: 0.65 mm
Female	6.0–8.5	0.70

With at most three ocelli, ill-defined. Anterior part of gonopods with two lateral and two mesial processes.

Distribution

British Isles: First found by the Brade-Birks in Whitehall Park, Darwen, Lancashire, on the surface of the soil under fallen leaves close to the edges of the flower beds and in rockeries in two other gardens of houses in the town, associated with *Melogona scutellare* (Brade-Birks, 1917c). The second occurrence was at Barrow-in-Furness, Lancashire (Brade-Birks, 1918a, X) in a garden, again associated with *M. scutellare.* A third record came from West Norfolk at Chivers Nurseries, Heacham (Brade-Birks, 1920c, XXV). In 1953, I found the species still flourishing in Whitehall Park, Darwen, under well embedded stones throughout the park. Mr. Adrian Baker found the species in an old ploughed potato field near Nordelph, Barroway, Drove, Norfolk, January 1970, in soil down to a depth of 12 inches near decaying potato tubers. More recently recorded by the survey from South Somerset (VC5) and East Sussex (VC14), by Dr. A. Rundle from Mid-Lancashire (VC60), and Mr. G. Fussey from Westmorland and North Lancashire (VC69).

Europe: France: Meurthe-et-Moselle, as *B. bradeae hussoni* Schubart and Husson, 1937; Germany: Botanic garden and cemetery, Berlin, as *B. verhoeffi* Schubart, 1930; Pasing, Bavaria, as *B. bluncki* Verhoeff, 1925; Sweden: Lund, graveyard; Kalmar, garden; Visby; as *B. bradeae* vars *elongata* and *trucata*, Lohmander, 1925. Schubert (1934) quotes a pers. com. from Lohmander suggesting that the Swedish varieties, *elongata* and *truncata* were not significantly different from *B. verhoeffi* and *B. bluncki* respectively, and that all these named forms were probably just examples of one species with highly variable gonopods.

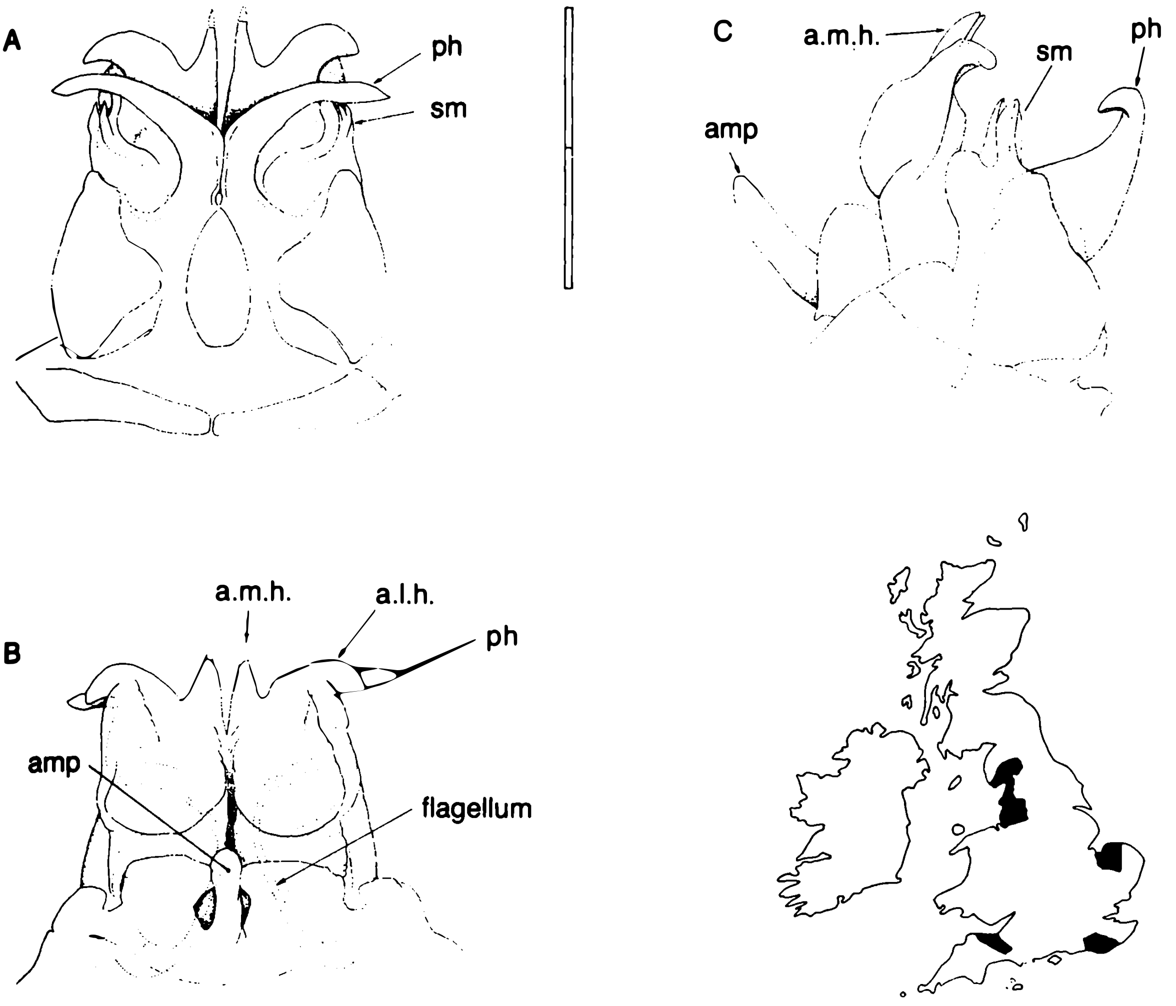


Fig. 23. *Brachychaeteuma bradeae.* A. Posterior view of the gonopod; B. Anterior view of the gonopod; C. Lateral view, from the right; *a.m.h.* anterior median horn; *a.l.h.* anterior lateral horn; *ph* posterior horn; *sm* solenomerite; *amp* anterior median process.

Brachychaeteuma bagnalli Verhoeff
(Fig. 24)

B. bagnalli Verhoeff, 1911: *Zool. Anz.*, *38*: 457–458
B. bagnalli char. emend. Brade-Birks, 1918: *J. Zool. Res.*, *3*: 50–53, Figs. 1–4

Adult Length: 7–8 mm (Verhoeff's original figures) Breadth: 0.5 mm
5–7 mm (more recent measures of fully contracted British individuals)

With never more than three ill-defined ocelli; anterior part of gonopods with two long diverging horn-like processes.

Distribution

British Isles: This was the first species of the genus and family described from a single male collected by Bagnall from Gibside, County Durham in 1911. Later rediscovered by Bagnall in three different Durham localities in 1918 (Bagnall, 1919), by myself in a garden in Easingwold, North Riding, a male in April 1956 and a female with two immature stadia (V and VIII) in August 1961. Most recently, Mr. Declan Doogue had a male and three females from a cornfield on the site of a deserted garden, St. Clare's Hospital, Ballygall, Dublin, December 1978. Mr. Adrian Rundle found the species at two sites in Westmorland and one in North Lancashire during the joint meeting of the British Myriapod and British Isopod Study Groups at Lancaster in April 1983, thereby adding two more vice-county records (60 and 69) to the existing two (62 and 66). Another individual found at this meeting by Mr. A. D. Barber in Westmorland shows variation towards the *bradeae* condition. *Macrosternodesmus palicola* was associated with Bagnall's animals at all his four sites, *Boreoiulus tenuis* at three sites, *Melogona scutellare* at two, and *Ophiodesmus albonanus* at one. The Easingwold animals were associated with *Blaniulus guttulatus* in an old potato patch.

Europe: This species has been recorded from caves in Belgium and northwest Germany (Westphalia) (Schubart, 1938).

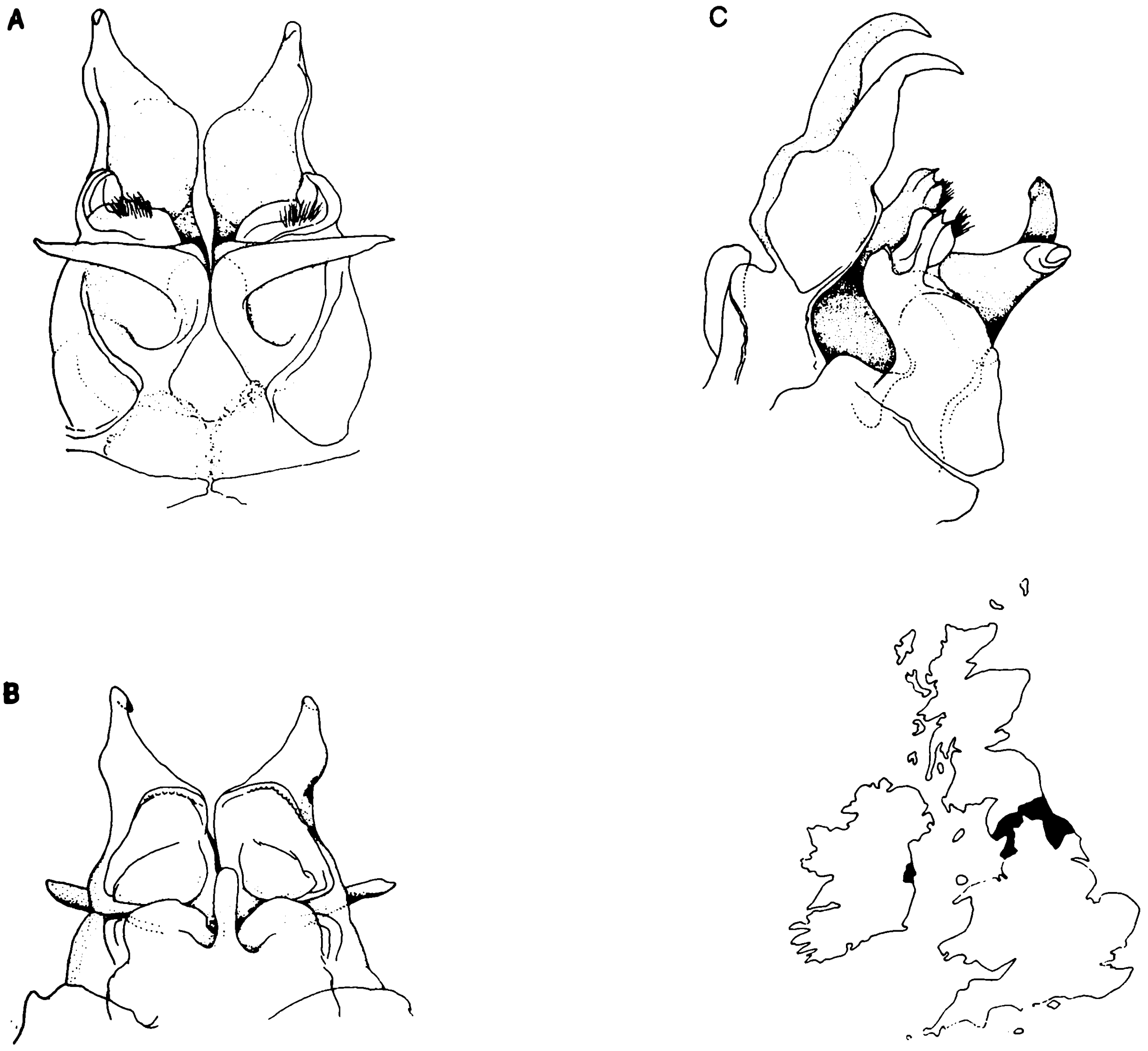


Fig. 24. *Brachychaeteuma bagnalli.* A. Posterior view of gonopod; B. Anterior view; C. Lateral view, from right.

Suborder CHORDEUMATIDEA

With the characters of the only family in the suborder:

Family CHORDEUMATIDAE

Cylindrical millipedes, slightly compressed laterally, without trace of paranota and quite unlike the Craspedosomatidea in general appearance. They do however have a number of important characters in common: 28 or 30 rings, three pairs of setae on each, spinnerets on the telson, undivided cheek lobes and the precise detail of the addition of ocelli to the ocular field stadium by stadium (p. 26, 68; Figs. 11 and 25). The chordeumatid gnathochilarium differs from that in the Craspedosomatidea in having an undivided mentum.

Chordeumatids differ most profoundly from the craspedosomatids and brachychaeteumatids in the constitution and arrangement of their gonopodal apparatus. On ring VII there is the reverse arrangement to that in the Craspedosomatidea: the anterior pair (8th) are peltogonopods and the posterior (9th) are the gonopods proper (Figs. 28, 29). However, unlike all other helminthomorphs, further limbs are modified and incorporated into a rather complex inseminatory apparatus; the hind limbs of ring VI (the 7th pair) and both pairs on ring VIII (pairs 10 and 11) are modified. Limbs 7 and 11 form anterior and posterior paragonopods respectively (Figs. 28, 29); limbs 10 are very much reduced. Verhoeff (1928) has described some of the details of this extraordinarily complex assemblage of modified limbs. Sperm is received from the genital openings on to the coxal sacs at the base of the posterior paragonopods; here the sperm mass is converted into a spermatophore which is then passed forwards to the gonopods proper to effect actual insemination. Often one picks up a male chordeumatid with the spermatophore held in the gonopods; in *Melogona gallica* it is green in colour and very obvious.

In the adult female chordeumatids there is a sternite without legs behind the second pair called the platosternite. This was regarded as a phylogenetic relic of the anterior pair of limbs on ring IV, but in fact, adult female chordeumatids have one fewer pairs of legs than female Craspedosomatidea (49 instead of 50 in species with 30 rings or 45 instead of 46 in species with 28 rings) and it appears that the platosternite is the remains of this pair of legs which is reduced in the last stadium, perhaps in association with the lengthened gonopodal region of the male (Blower, 1978).

The family is represented in Britain by two small to medium sized species of *Chordeuma* and two smaller species of *Melogona* (= *Microchordeuma*).

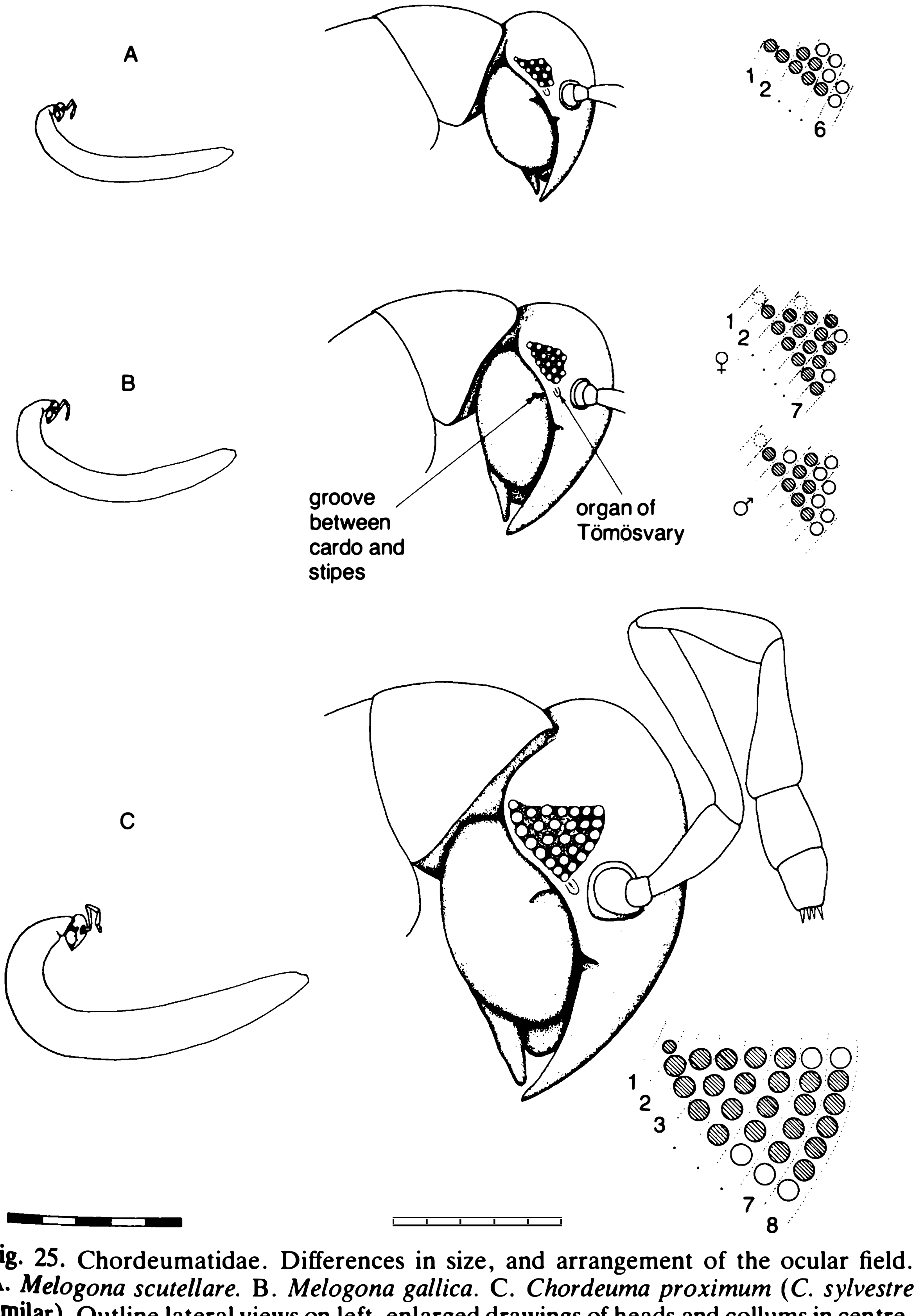


Fig. 25. Chordeumatidae. Differences in size, and arrangement of the ocular field. A. *Melogona scutellare.* B. *Melogona gallica.* C. *Chordeuma proximum* (*C. sylvestre* similar). Outline lateral views on left, enlarged drawings of heads and collums in centre, and further enlargements of the ocular fields on right, partly diagramatized to indicate variation in the additions of successive rows of ocelli into the field. In the centre figures note the organ of Tömösvary at the anteroventral apex of the ocular triangle; note also the cheek lobes with only a trace of a division into separate cardo and stipes.

In the right-hand figures, cross hatched ocelli are invariably present, open ocelli may be absent on one or both sides, dotted open ocelli are very rarely present – as, for example, the ocellus representing the first row in older stadia of *M. gallica.*

Key to British species of Chordeumatidae

1. Adults larger than 10 mm long and 1.1 mm diameter (height). Well pigmented. Ocelli in an almost equilateral triangular field (Fig. 25c).
Stadia VI, VII, VIII and IX with *at* least
10 15 20 24 ocelli **2**

Adults smaller than 10 mm long and 0.9 mm diameter (height). Lightly to moderately pigmented. Ocelli in more acute triangular field (Figs. 25A and B); never more than 3 or 4 in a row (at right angles to ventral edge of head capsule (Fig. 25).
Stadia VI, VII, VIII and IX with *at most*
7 11 15 17 ocelli **3**

2. Visible apex of gonopod pointed. (Fig. 26) ... *Chordeuma sylvestre* (p. 87)

Visible apex of gonopod broad and hatchet-shaped. (Fig. 27) ....
.... *Chordeuma proximum* (p. 90)

3. Larger, adult males 8.0 mm long, 0.75 mm diameter (height) or larger; females slightly larger still. Moderately pigmented. Adults with 30 rings. 8–17 ocelli in 6 or 7 rows; females with three of these rows with 3 ocelli, males with up to three, with 3 ocelli; either sex may have four ocelli in one or two of these rows; often more than one ocellus in the last (most anterior) row. (Figs. 25B, 28) .... *Melogona gallica* (p. 92)

Smaller, adult females 8.0 mm long, 0.75 mm diameter (height) or smaller, males smaller still. With very little pigment, amber to cream colour. Adults with 28 rings. 7–12 ocelli in 5 or 6 rows. Two of these rows may have up to 3 ocelli; usually only one ocellus in the last (most anterior) row, if present. (Figs. 25A, 29) ....
.... *Melogona scutellare* (p. 94)

Chordeuma sylvestre C. L. Koch
(Fig. 26)

Chordeuma sylvestre C. L. Koch, 1847: *Syst. der Myriapoden,* 124

Adult	30 rings	Male	Length:	10.8–12.4	Diameter:	1.19–1.29
(stadium IX)	incl. telson	Female	(mm)	11.2–13.4	(mm)	1.35–1.53

Diameters measured are heights which are approx 1.2 times width. Brolemann (1935) gives almost identical measurements of width but those of Schubart (1934) extend up to 1.8 mm. Both authors give lengths up to 18 mm but this may be due to their measuring extended individuals.

Medium to dark brown dorsally, mottled laterally and much lighter ventrally. Almost identical in appearance to *Chordeuma proximum.* Ocelli idealy in an equilateral triangular group but with a single ocellus representing the first two rows, the first, extra to and slightly ventral to the posterior apex; often one or two ocelli missing from the extremities of the last three rows. Males varying thus between 24 and 29 ocelli, females between 26 and 29, in total.

Haacker (1971) describes the occurrence of glands opening mid-dorsally on ring XVI of the male. The cuticular modifications are characteristic of the species and differ from the similar structures in *C. proximum.* The glands secrete a pheromone attractive to the female during courtship.

Biology. The August population at Trelil (see below) consisted entirely of stadia VII and VIII, the following April there were adults (stadium IX) in abundance but also newly hatched stadia II and III and also stadia IV, V, VI and VII. In April of the next year (1963, after a rather severe winter) there were adults and stadia III, IV and V. In the complete absence of adults in the autumn, I presume that there must have been an extended period of egg-laying from early in the year right through to April, to account for the wide stadial spectrum in April.

Distribution

British Isles: I found this species in a mixed deciduous wood by the village of Trelil in north Cornwall in August 1961 but had to revisit the site the following April to secure adults and determine the species. The sub-adults (stadium VIII) in autumn ranged widely over a large area of the wood but the adults and young in spring were severely restricted to the bottom of the slope, especially in an accumulation of leaf litter against the dry stone wall at the boundary of the wood with the road. Mr. R. Daniels sent me some Tullgren extracted material from immediately neighbouring sites in April 1975 which contained an abundance of this species, mainly stadia IV and V but a few at III and VI. A second locality for the species was found by Mr. Barber at the Easter meeting of the British Myriapod Group in 1982, in the southern part of East Cornwall (VC2).

Europe: Whilst this species has the most restricted distribution of our four chordeumatids, its European range is wider than that of the other British representatives. France, Holland, Belgium, Switzerland, Germany and Italy (as far south as Calabria); also recorded by Lang (1954) from Czechoslovakia, and by Lokshina & Golovatch (1979) from the Soviet Carpathians. Lang figures the animal and it is quite evident that his concept of *C. sylvestre* is, in fact, *Orthochordeumella germanicum*. Schubart (1934) and Hoffman (1979) refer to this problem. The animal referred to here is that figured and described by Latzel (1884) and Broleman (1935).

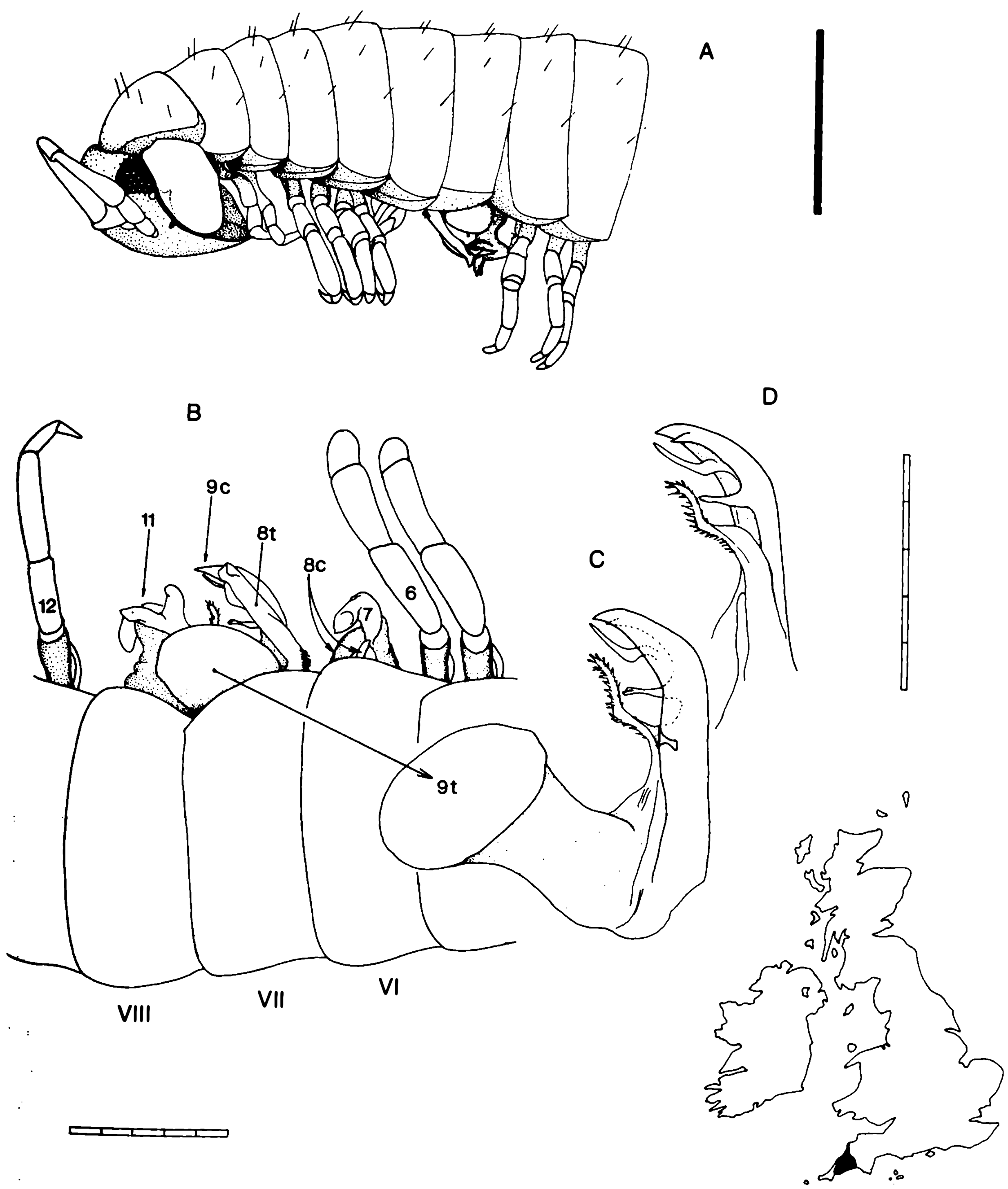


Fig. 26. *Chordeuma sylvestre.* A. Head and rings I to IX of mature male; B. Ventral part of rings VI to VIII of male showing gonopodal apparatus *in situ*: from anterior to posterior, anterior paragonopods (limbs 7), peltogonopods (limbs 8); gonopods proper (limbs 9), posterior paragonopods (limbs 11) (limbs 10 are vestigeal); the qualifying letters, *c* and *t*, denote coxal or telopodite derivatives. C. Isolated left gonopod in external profile; D. Apex of the coxal pillar of the right gonopod, internal profile. Compare the gonopods with those of *C. proximum* (Fig. 27), noting the long spiny flagellum and the distinctly pointed apex of the coxal pillar (9c) which is clearly visible *in situ* and serves to distinguish *sylvestre* from *proximum* immediately.

Chordeuma proximum Ribaut
(Fig. 27)

Chordeuma proximum Ribaut, 1913: *Bull soc. Hist. nat. Toulouse 46*: 33–36 Figs. 20–28

Adult (stadium IX)	30 rings incl. telson	Male	Length: 10.8–10.9 mm (extended males up to 12.8 mm)	Diameter: 1.16–1.25 mm
		Female	12.0–12.7	1.38–1.53

Description exactly as *C. sylvestre* for colour and arrangement of ocelli, but distinguishable by the detailed structure of the gonopods (Fig. 27), and the shape of the dorsal region of ring XVI in the male where the dorsal glands open (see note on *C. sylvestre*, p. 87).

Biology: Apparently, like the other chordeumatids, an annual in the south at least. In Gower, south Wales, adults appear by the end of September but with some individuals remaining in stadia VI, VII and VIII, mainly VIII. In the Forest of Dean, the most northerly record for the species here, in late March and early April there is a mixture of stadia VI, VII and IX which is suggestive of a two-year life cycle.

Distribution

British Isles: First found by Satchell in the Forest of Dean (1955) and recorded by Nelson (1964). It now occurs at several sites in Dean and has been found in Gower (Bishops wood, Caswell, 1967) and later in other Gower localities, also in West Sussex and Surrey (Kime, 1968) and South Devon (Kime, pers. com.). The history of its occurrence in Gower is interesting: it was first seen at Bishops wood, by Caswell in September 1967 and later at Coed Abertawe (by Llethrid) in September 1969. A site at this last locality had been under observation from 1965 and was sampled regularly since March 1968; *C. proximum* did not appear in the Tullgren extractions until the sample of September 1971 (17 animals in 20 units of 0.1 m^2). In September 1972 it fell into pitfall traps on the site. Recently Mr. Alloyan had the species in pitfalls on spoil heaps in the lower Swansea valley. Most recently from Bedford (VC30), Merioneth (VC48) and Brecon (VC42).

Europe: Only recorded from France; from Orne, Maine-et-Loire and Mayenne in the northwest, Puy de Dôme, Tarn, Aveyron in south central and Pyrénées-Orientale in the south.

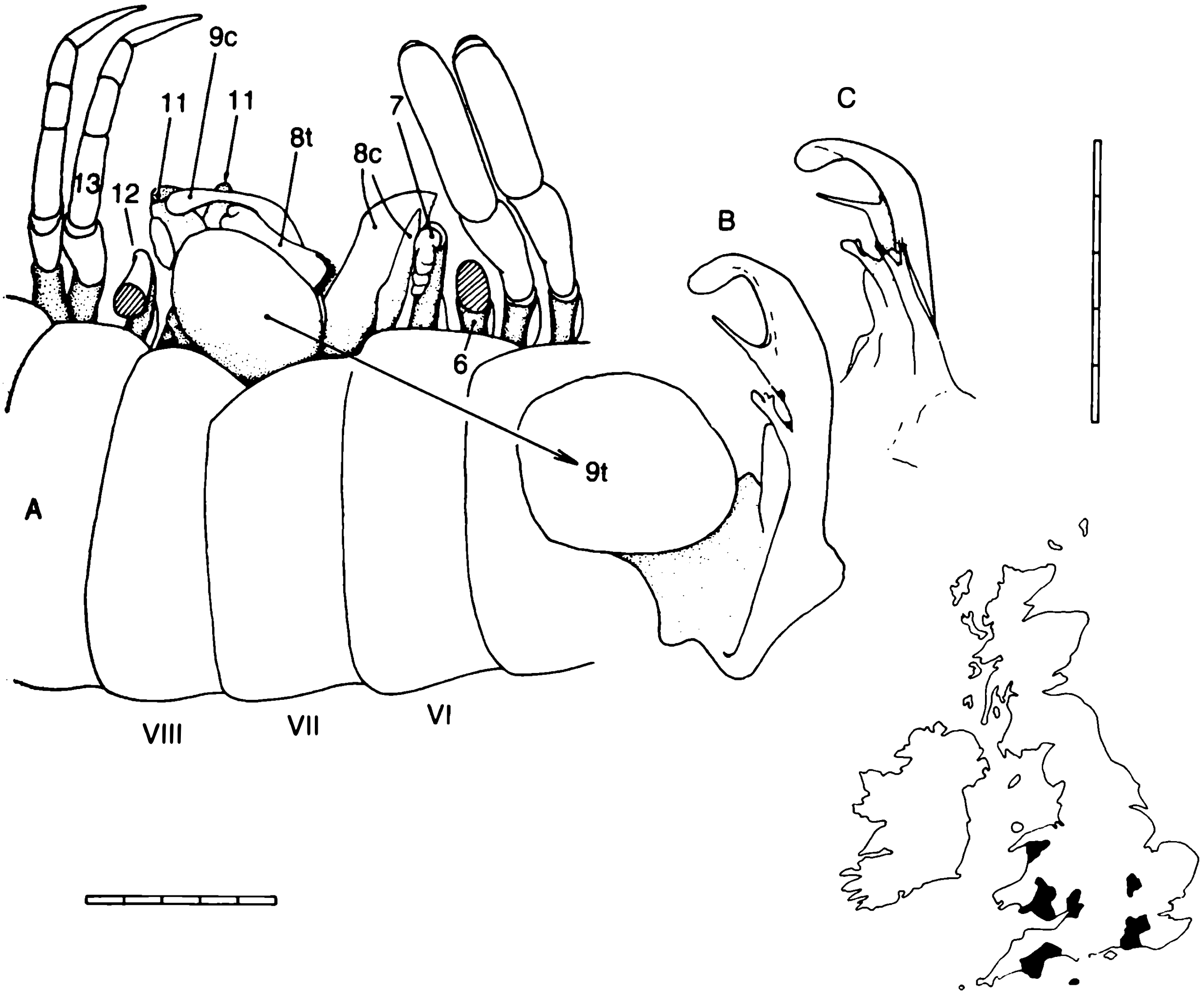


Fig. 27. *Chordeuma proximum*. A. Lateral view of rings VI to VIII of male showing gonopodal apparatus *in situ*; numbers indicate the limb pair modified, the qualifying letters *c* and *t* denote coxal or telopodite derivatives; see also legend to Fig. 26B; B. Isolated left gonopod in external profile; C. Apex of coxal pillar of right gonopod, internal profile. Limbs 6 and 12 have been removed to obtain a clearer view of the gonopods. Compare with gonopods of *C. sylvestre* (Fig. 26) noting that in *proximum* the pseudoflagellum is smaller and bifurcate, and the spatulate apex of the coxal pillar of the gonopod (9c) clearly visible *in situ* and quite distinct from the pointed apex in *sylvestre*. The more prominent coxal process (8c) of the peltogonopods in *proximum* are merely a feature of this particular individual which was more contracted than the individual of *sylvestre* (Fig. 26).

Melogona gallica (Latzel)
(Fig. 28)

Chordeuma gallicum Latzel, 1884: *Bull. Soc. Amis. Sci. Natur. Rouen* 1883: (2) *269*: Pl. 1, Figs. 4–5

Microchordeuma gallicum of Blower (1958)

Adult	30 rings	Male	Length: 7.9 mm	Diameter: 0.75–0.85 mm
(stadium IX)	incl. telson	Female	7.8–10	0.84–0.96

(diameters measured are heights, which are 1.2 × width approx.)

8–17 ocelli in the males, 14–18 in the females; usually in seven rows but the single ocellus of the first row is often indistinct. Usually three rows of the female or up to three rows of the male, with at least three ocelli; one or two of these rows may have four ocelli. Usually with more than one ocellus in the last (seventh) row.

More evenly pigmented than *M. scutellare*, medium to dark amber colour. The gonopods of preserved adult males are usually very prominent and frequently hold a distinctly black spermatophore.

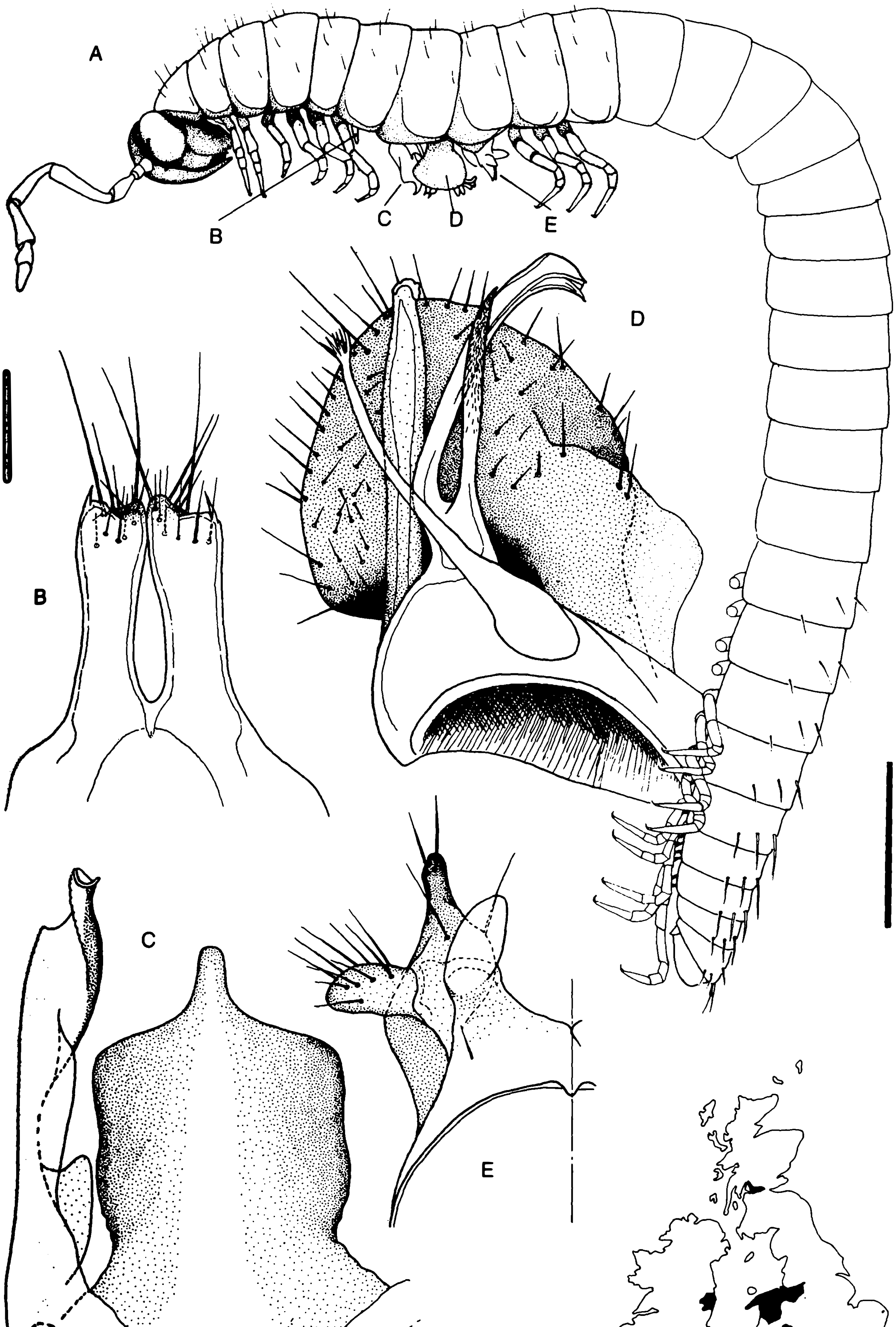
Biology. On sorting through some Tullgren samples from Delamere forest in Cheshire in April and May 1975, Dr. Erwin Meyer found adults (stadium IX) and stadia VII and earlier which is rather suggestive of a two-year cycle; more details are needed to be certain.

Distribution

British Isles: First found and recorded as British in garden debris at Beddgelert, Caernarvonshire (Eason, 1957). I found a flourishing population amidst litter in a rather dampish alder carr at Coldrinnick, Camel Valley, Cornwall, 1963 and the species was found on two of the field meetings of the British Myriapod Group at Devon, 1970 and Herefordshire, 1971. Eleven further county records have been added during the last twelve years, the most recent from Middlesex, Holland Park by Davis (1979) and the first record for the Irish Republic, from Wicklow collected by Mr. D. Doogue, 1982. Before the British Myriapod Survey the species was ranked 45th; it is now the 27th.

Europe: North and Central France; recently from Haute Garonne in the south (Mauriès, 1960). Holland, Belgium, Switzerland, Luxembourg and Germany west of the Rhine. Most recently from around Bergen in Norway (Meidell, 1968) where it is regarded as an introduced species.

Fig. 28. *Melogona gallica.* A. Adult male showing gonopods *in situ.* Note the metazonite setae which become longer and stronger, and move more in line, towards the tail. The paired spinnerets are shown just dorsal to the anal valves; B. Anterior paragonopods, anterior view (modified limb pair 7); C. Peltogonopods, (limb pair 8), anterior view; D. Left gonopod (limb pair 9), internal profile; E. Posterior paragonopods (limb pair 11), posterior view. (B – E from Blower, 1957. Compare with Fig. 29.)


A
B
C
D
E
D
B
C
E

Melogona scutellare (Ribaut)
(Fig. 29)

Chordeumella scutellare Ribaut, 1913: *Bull. Soc. Hist. Nat. Toulouse 45*: 93–96, Figs. 1–9
Microchordeuma scutellare of Blower (1958)

Adult	28 rings	Male	Length: 5.6–6.7 mm	Diameter: 0.55–0.60 mm
	incl. telson	Female	6.6–8.0	0.70–0.75

(diameters measured are heights, which are 1.2 × width approx.)

Almost without pigment; slight touches of amber in the dorsal parts of the rings grading to cream-white ventrally. 7–12 ocelli in five or six rows; usually only one ocellus in the sixth row, if present; never more than three ocelli in a row, usually in the fourth and fifth rows.

The anterior paragonopods and the median plate of the peltogonopods are variable and two subspecies had been described. These subspecies were found to coexist sympatrically and are therefore to be regarded as varieties (see Blower, 1957).

Biology. Details of the life history are given by Blower (1979) from sites in South Wales and Derbyshire. In Gower, S. Wales, stadium III appears at the end of March and adults (stadium VIII) appear by October. In Derbyshire, stadium III does not appear until mid May and most individuals are still in stadium VII by October. This slight retardation in the north does not seem disadvantageous, the life cycle is completed within the year in both northern and southern sites where similar adult densities of 30–40 per square metre are found.

Distribution

British Isles: Quite a common species in woodland litter and soil, in hedge bottoms garden debris and occasionally under stones and bark. It is quite small, active and easily overlooked or lost. Since this is an annual species, adults are completely absent during the summer months.

First recorded from Lancashire (Brade & Birks, 1916). Now there are records from 28 of the 70 vice-counties of England and Wales. The species probably occurs throughout these countries with the possible exception of the drier south eastern counties. It has recently been found in County Kerry in the extreme south west of the Irish Republic.

Europe: Only from the type locality at Grenoble, Isère and Haute-Garonne in Southern France, and Piedmont in Northern Italy, the latter as *M. scutellare taurinorum* Verhoeff.

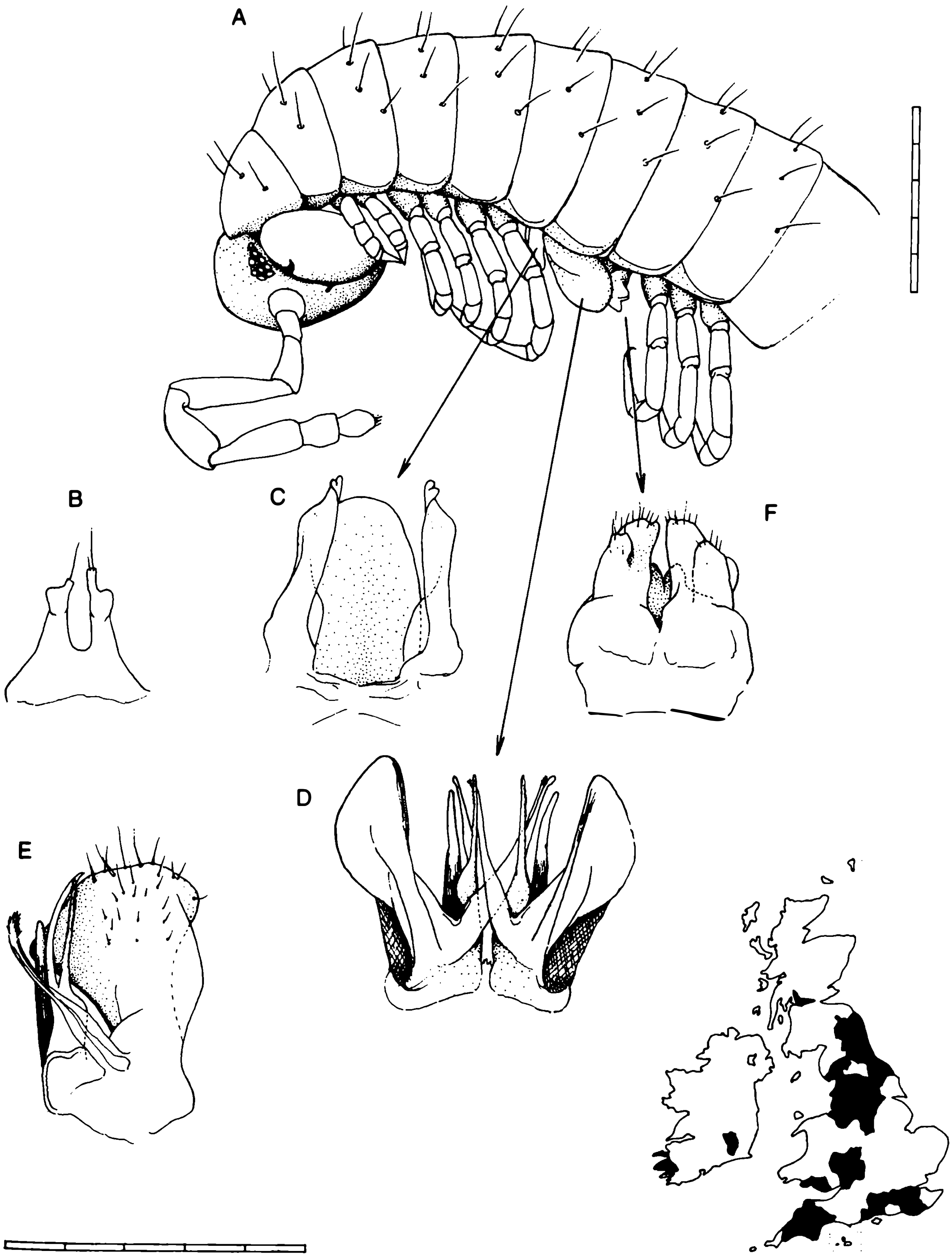


Fig. 29. *Melogona scutellare.* A. Head and rings I to IX of an adult male to show gonopods *in situ.* B. Anterior paragonopods (limb pair 7), anterior view; these are not usually visible in a lateral view as at A. C. Peltogonopods (limb pair 8), consisting of a median coxal plate, convex anteriorly, and lateral telopodites, in posterior view. D. Gonopods proper (limb pair 9), posterior view showing lobe-like telopodites (the only parts visible in lateral view) and inner coxal derivatives: an anterior pillar, an intermediate bifurcate lobe and a posterior pseudoflagellum; each pseudoflagellum crosses to the other side where their apices lie juxtaposed to the curved unarmoured branch of the bifurcate lobe. E. Left gonopod internal profile. F. Posterior paragonopods (limb pair 11), posterior view.

Subclass HELMINTHOMORPHA

Order JULIDA

Just half of the British species of diplopods belong to this large order of snake millipedes. The order comprises the wider bodied Julidae (18 British species) together with the more slender Nemasomatidae and Blaniulidae (8 species). Demanage (1981) gives separate ordinal status to the Julidae on the one hand and to the Nemasomatidae and Blaniulidae on the other. Here the more usual scheme is adopted, using a single order to encompass all these groups, following Hoffman (1979).

With or without ocelli. Cheeks clearly divided into proximal cardines and distal stipetes, the ventral edges of which may be produced in adult males. The collum is large and overlaps the head in front and the second ring behind. Trunk cylindrical, paranota never developed. Metazonites with longitudinal striae or flutings, at least around the ventral half of the ring. Metazonite setae, if present, forming a whorl fringing the posterior edge of the ring. Ozopores present mid-laterally on the sixth to the last podous ring. All rings except the collum and the second are closed ventrally, either by the union of the ventral tips of the pleurotergal arch (ring III), or by the incorporation of the sternites into a rigid cylinder. In Julidae and Blaniulidae the sternites are fused to the pleuro-tergal arch; in the Nemasomatidae, they are not fused, but are firmly held between the ventral edges of the arch and are not moveable or displaceable in an antero-posterior sense as are the sternites of Chordeumatida.

All stadia possess an odd number of pairs of legs. The increment of podous rings added at a moult may vary both within the stadium or between stadia (Table 1 and Figs. 8 and 9) As a consequence of this, a given stadium is characterized by a range of numbers of rings and a given number may be common to several stadia. The stadium in which maturity is achieved can also vary and there may be a succession of adult stadia. In the case of males this succession is rarely direct (*Nemasoma varicorne* and *Cyclindroiulus nitidus*); more usually it involves the interpolation of intercalary males (periodomorphosis), in some Blaniulidae and Julidae. For these various reasons adults are represented by several stadia which themselves include a range of segment number, and the total range within an adult may be as great as 20 rings. The total number of rings in the adult, including the apodous rings and telson is usually greater than 30, but occasional individuals of *Nemasoma varicorne* may mature as early as stadium V with as few as 23 rings, *Proteroiulus fuscus* may mature at stadium VI with 26 rings and *Brachyiulus pusillus* may mature at VII with 29 rings.

In Julidae and Blaniulidae the first pair of legs in the mature male are metamorphosed into a pair of hook-like structures (except in *Julus*) and there may be modifications to the coxae of the second pair; on the succeeding legs of the male there are sometimes special pads (Fig. 5B) (Julidae) or lanceolate setae (Blaniulidae) to facilitate pairing. Both pairs of limbs on ring VII are modified as gonopods. The anterior pair (8) form protective peltogonopods and the hinder pair (9) form the gonopods proper, the actual organs of intromission. In the Blaniulidae and Nemasomatidae, both pairs stand proud of the ventral side, posteriorly directed, resting between leg-pairs 10–13 (Figs. 36, 37, 38). In the Julidae the gonopods are wholly (or partially in *Brachyiulus pusillus*) retracted within the lumen of ring VII and the only indication of their presence is a gap in the podous series.

In the species descriptions which follow (pp. 100–187) the numerical data at the head of the description are, in order:

Stadia in which maturity is achieved for adult males followed by that for females.	Range of podous rings	Range of lengths (mm)	Range of diameters (mm)

Key to British families of JULIDA

1. Ocelli may occupy a triangular field (Nemasomatidae, Figs. 30A, B; 31 and 32) or form a single line (in the antero-posterior sense, parallel to the ventral edge of the head capsule), (Fig. 30E, F, G) or a single line augmented anteriorly by two or three extra ocelli (older stadia of *Proteroiulus fuscus*) (Fig. 30C, D), or completely absent. Longitudinal striae confined to the ventral half of the ring up to the level of ozopores (Figs. 32, 33). Longer and thinner; length: breadth ratio, males 20–30:1, females 15–30:1 (except *P. fuscus*, 12:1 and 15:1 respectively); adults usually thinner than 0.7 mm (except *P. fuscus*, males up to 0.7 mm, females up to 0.9 mm). Never with caudal projection. Gonopods never retracted into the lumen of the seventh ring **2**

Ocelli usually present in a triangular field (Figs. 1, 12), absent from only two rare species, *Metaiulus pratensis* (confined to the south east) and *Cylindroiulus vulnerarius*. Longitudinal striae or flutings extend all around the ring (Figs. 1, 12); a distinct suture divides the prozonite from the metazonite. Shorter and fatter; length: breadth ratios of males (always the more slender sex) 10–14:1 (except *Leptoiulus kervillei*, 20:1). Adult males usually thicker than 0.7 mm (but *Enantiulus armatus* and *Metaiulus pratensis* may be as slim as 0.6 mm). With or without caudal projections. Gonopods usually completely retracted within the lumen of the seventh ring (except *Brachyiulus pusillus*) ....JULIDAE (p. 122)

2. Ocelli occupying an equilateral triangular field (Figs. 30A, B; 31, 32) ....NEMASOMATIDAE (p. 98)

Ocelli absent, or in a single antero-posterior line, with or without two or three additional ocelli in a second line anteriorly, by the antennal base ....(Fig. 30C–G). BLANIULIDAE (p. 105)

Family NEMASOMATIDAE

Nemasomatids are indeed 'thread-like bodies' with length: breadth ratios of males ranging from 29:1 to 24:1 and in females, 22–24:1, but are not more attenuated than blaniulids. Although their inclusion within the order Julida may suggest they are monozonian, nemasomatids are, in fact, trizonian; their sterna are not integral with the pleuro-tergal arches but merely fit tightly between the ventral edges of the arches to give the impression that they are parts of complete cylindrical sclerites.

Like blaniulids, there is no definite suture between the narrower prozonite and the wider metazonite; the longitudinal striae extend across onto the prozonite but are limited to the ventral half of the ring up to the level of the ozopores. The pre-anal ring is never produced into a caudal projection. The animals are only moderately pigmented; the dark contents of the ozadenes contrast with the lighter trunk.

The first pair of legs in the males are not modified as those of blaniulids and julids; they are a little shorter, with only five podomeres and carry a long setose projection on the penultimate podomere. In *Thalassisobates littoralis* males there is a projection and pit on the femora of leg pairs 4–7 which may function in an analagous manner to the lanceolate setae of the blaniulids.

As in blaniulids the gonopods stand proud of ring VII and the anterior peltogonopods consist of median coxal projections and lateral single-jointed telopodites; the posterior gonopods differ from those of blaniulids and are more julid-like in possessing a distinct coxal base and a flagellum orginating from the peltogonopods (Figs. 31, 32).

The two British representatives of this family are each distinctive; *Nemasoma varicorne* is parthenogenetic in Britain and an obligate inhabitant under bark; *Thalassisobates littoralis* as its names indicate, is a truly marine millipede living between tidemarks on the sea shore.

Key to the British species of Nemasomatidae

1. Usually less than 0.5 mm diameter; setae fringing metazonites short and difficult to see; tarsal claw half the length of the tarsus. Usually found under the bark of standing or fallen trees or stumps. (Fig. 32) .... *Nemasoma varicorne* (p. 102)

0.5–0.7 mm in diameter; setae fringing metazonites distinct; tarsal claw equal in length to the tarsus. Exclusively littoral, at or below high water mark. (Fig. 31) .... *Thalassisobates littoralis* (p. 100)

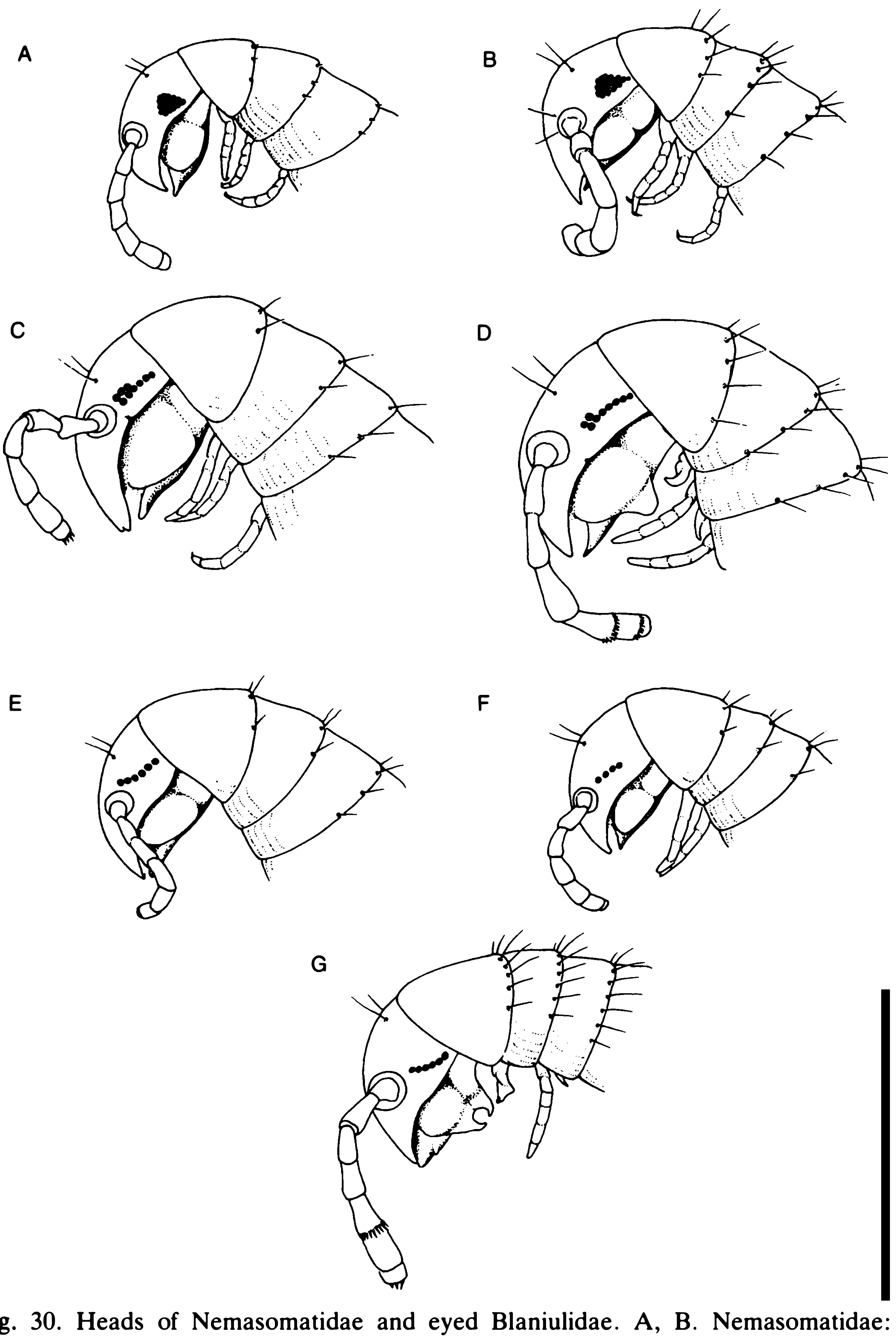


Fig. 30. Heads of Nemasomatidae and eyed Blaniulidae. A, B. Nemasomatidae: A. *Nemasoma varicorne*; B. *Thalassisobates littoralis*. C–G. Blaniulidae: C. *Proteroiulus fuscus*, adult female; D. *P. fuscus*, adult male; E. *P. fuscus*, stadium with 6 ocelli; F, *P. fuscus*, stadium with 4 ocelli; G. *Choneiulus palmatus*, adult male. Note the short metazonite setae in *Nemasoma varicorne*; there is a single line of ocelli in juvenile *P. fuscus*, but *C. palmatus* is distinguishable by the larger number of metazonite setae.

Thalassisobates littoralis (Silvestri)
(Fig. 31)

Isobates littoralis Silvestri, 1903: *Acari, Myriopoda et Scorpiones*, *99* (*9*), Figs. 1–10

Male	(30)36–42(56)	Length:	9–12(16) mm	Diameter:	0.50 mm
Female	37–48(59)		11–17(21)		0.54–0.70

(Schubart's figures in brackets)

Colour similar to *Nemasoma varicorne*, pale greyish white with dark brown ozodenes. Setae fringing metazonites quite prominent.

Schubart (1934) lists animals with many more segments than British individuals. His reference to ocelli (12–27) suggests that his animals were adult from stadium VI but the youngest adults from Britain (Isle of Man) were probably stadium VIII males and IX females.

Distribution

British Isles: First recorded from Grange-over-Sands, Lancashire, by Bagnall (1916) who found a single female under a stone beneath high water level together with specimens of *Strigamia maritima.* This was the only record available at the time of Blower (1958). The species has been found at four stations since it went to press: Eason (1957) records several specimens of both sexes in shingle between tide marks in the Menai Straits 1.5 Km west of Caernarvon in Wales, May 1954. I found four males, six females and three immatures at Port St. Mary, Isle of Man, 30th August 1959. The animals were under stones between high water neap and high water springs, in fine gravel associated with two species of littoral centipedes *Geophilus fucorum* and *Strigamia maritima.* More recently the species was found at Slapton in Devon, on the seaward side of the shingle ridge, in pitfall traps, in 1974 by Dr. M. J. Cotton, and in 1977 by Mr. Paul Harding. Mr. W. A. Ely identified the species in material in the Leicestershire Museum, collected at Blakeney Point, Norfolk in 1972 (see Harding, 1983).

Europe: The species occurs on the Mediterranean shores of France (three localities), Monaco (one), Italy (three), Yugoslavia, Sicily, Sardinia, Corsica and Algiers. Also, from Sweden.

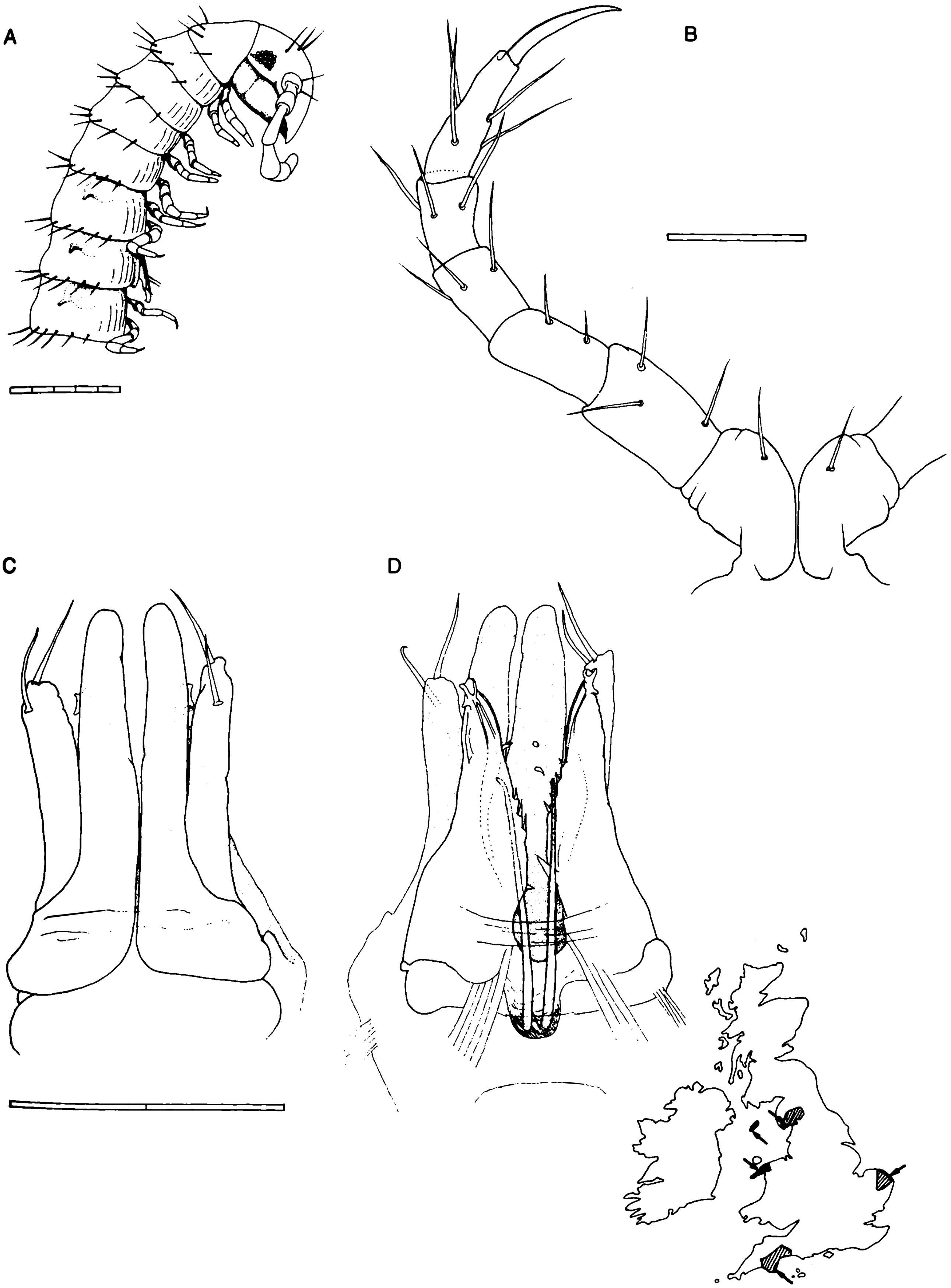


Fig. 31. *Thalassisobates littoralis*. A. Head and first eight rings of an adult male; B. Leg pair number 23 (from ring XIV) to show the claw which is nearly as long as the tarsus; C. The ensemble of peltogonopods and gonopods proper, from in front; D. The same, seen from behind.

Nemasoma varicorne C. L. Koch
(Fig. 32)

Nemasoma varicorne C. L. Koch, 1847: *System der Myriapoden*, *116*, pl. 2, Fig. 28.
Isobates varicornis (C. L. Koch) of Blower (1958)

Male	V–X	19–35(37)	Length: 4–13 mm	Diameter: 0.33–0.45 mm
Female	VI–XIII	22–40(50)	5–11(14)	0.40–0.50

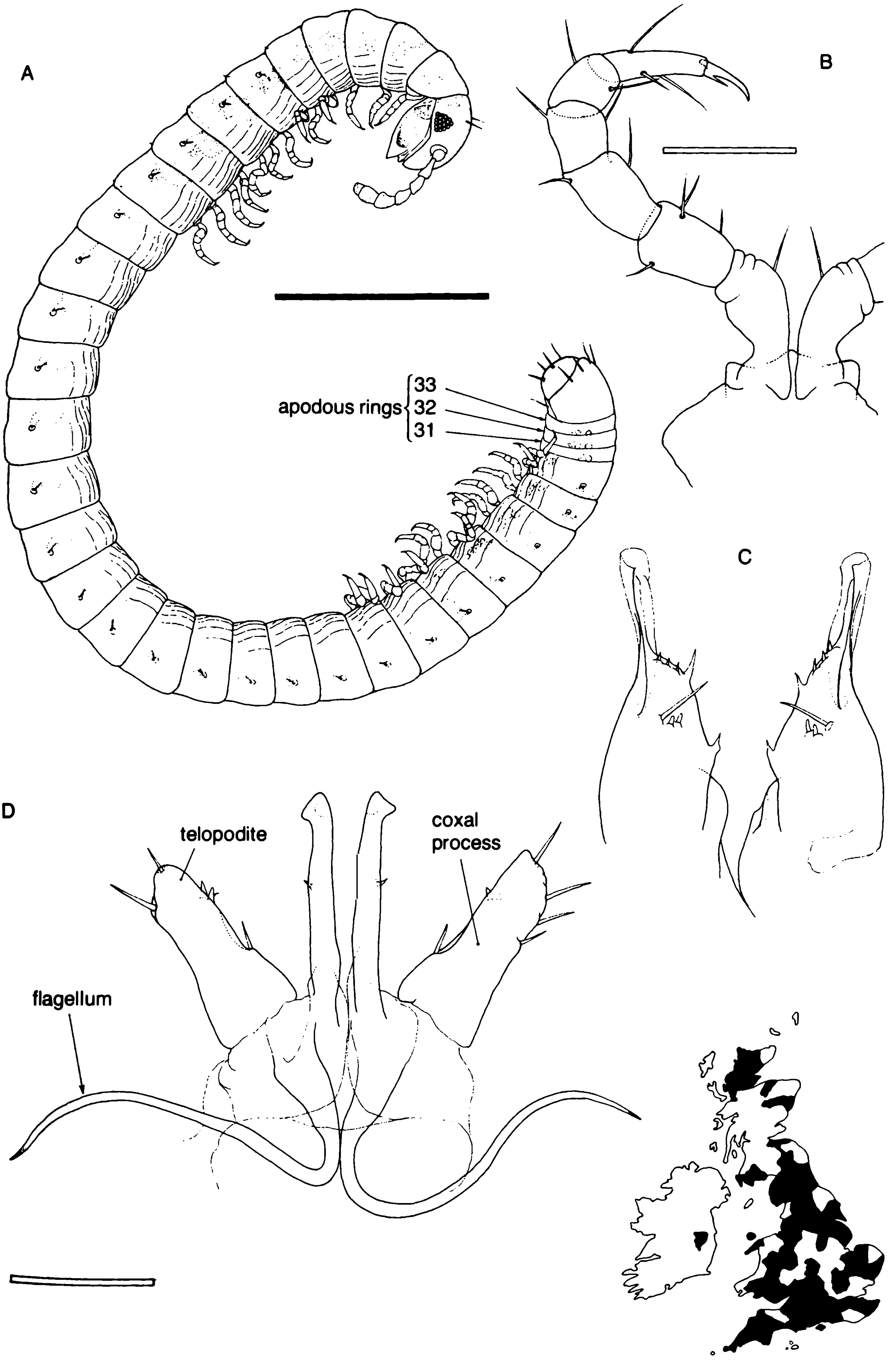
(male dimensions from Schubart)
(brackets extend data to Schubart's limits)

Greyish white, with dark brown ozadenes; setae fringing metazonites very short and hardly noticeable. Easily distinguished from its frequent associate beneath bark, *Proteroiulus fuscus*, by the very short setae, lighter colour, its julid-type triangular group of ocelli and its small diameter (*Nemasoma* = 'thread-like body'). In life, the ozadenes are dark yellow; in *P. fuscus* they are red.

Biology. In the British Isles males are usually absent but Brookes (1963) had 17 males amongst the several thousand females he handled; he reared these males and observed that mature males moulted directly into mature males of the next stadium (that is, with the gonopods of the mature male). Males are rarely found amongst the small numbers encountered in general collections but I had four amongst a total of 44 mature animals from a site in the Cotswolds. Enghoff (1976a & c, 1978a & b) gives details of the sexual biology of this species in Europe; a normal bisexual form occupies central Europe; this is surrounded on the west, north and east by a parthenogenetic form in which males are extremely rare and probably non-functional. Dr. Enghoff has examined the material from the Cotswolds mentioned above and found them to belong to the parthenogenetic form.

Brookes (1963, 1974) gives details of the anamorphosis and life-cycle of this species in a Cheshire wood. Females lay eggs singly throughout spring and summer; these develop without fertilization to stadia II, III and exceptionally IV by their first winter; eggs laid late in the season may only get as far as stadium I and winter is spent in this stadium; this is the only known instance of individuals of stadium I being able to feed and survive over winter. The second growing season takes the population to stadia V and VI

Fig. 32. *Nemasoma varicorne*. A. Adult female with 30 podous and three apodous rings; the legs of the mid-trunk region are omitted from the drawing; ozopores can be seen on all podous rings from VI to the last (XXV) and embryonic pores on the three apodous rings. Longitudinal striae are confined to the ventral halves of the rings (a character of the Nemasomatidae and of the Blaniulidae). The ocelli form an equilateral triangle (character of British Nemasomatidae). B. Leg pair number 22 (from ring XIV) showing the claw, which is about half the length of the tarsus (compare with Fig. 31B); C. Gonopods from behind; D. Peltogonopods from behind.


A
B
C
D
apodous rings
33
32
31
telopodite
coxal process
flagellum

(exceptionally VII) by the second winter. Females mature first at stadium VI (23–25 podous) and thus the shortest period between egg and egg is two years.

Distribution

British Isles: First recorded by Bagnall (1912b) from under fir bark in Durham and Northumberland. In Blower, 1958 there were records from 13 vice-counties; a further 10 were listed by Blower (1972) since when, the number of vice-counties known to be ocupied has more than doubled; this is one of the most spectacular result of the activities of the British Myriapod Survey. The records now extend from West Sutherland in the north, to West Cornwall in the south west and Kent in the south east. At the time of writing, there is only one record from Ireland. Records are almost exclusively from under bark of both coniferous and deciduous trees where the species is often associated with *Proteroiulus fuscus, Cylindroiulus punctatus* and *C. britannicus*.

Europe: Enghoff (1976c) provides a map of the distribution of both thelytokous (parthenogenetic) and bisexual forms in Europe. The bisexual form occurs from northern Italy, NW Yugoslavia and NW Romania in the south, through Austria, Germany (mainly south, east and north), and Czechoslovakia to southern Denmark and Poland in the north. The thelytokous form surrounds the central European bisexual form to the west, north and east, i.e. Britain, France and the Netherlands in the west, northern Denmark, southern Norway, Sweden and Finland in the north, the Soviet Union, central Romania and Yugoslavia in the east.

At the boundary between the two forms, both may occur in the same locality, especially in southern Denmark, but also in west West Germany, Holland and Lithuania.

Family BLANIULIDAE

Like the appropriately named Nemasomatidae, blaniulids are also long and thin julidans; the length:breadth ratio of males ranges from 20:1 to 30:1 and of females, from 15:1 to 30:1. *Proteroiulus fuscus* is exceptional with length:breadth ratios as high as 12:1 in males and 15:1 in females; the ratios for male julids range from 10:1 to 14:1. The smallest males of *Leptoiulus kervillei* have the build of a blaniulid with a ratio of 20:1.

Like julids and unlike nemasomatids, blaniulids are monozonian with sternites intimately fused to the pleuro-tergal arches. Unlike nemasomatids, blaniulids are not appropriately named, three of the six species listed possess eyes. Like nemasomatids, there is no definite suture between the pro- and metazonites; the longitudinal striae extend on to the prozonite but are restricted to the ventral half of the ring; there is never a caudal projection from the pre-anal ring. The eyed species are moderately well pigmented but the blind species are pale; in all blaniulids the ozadenes stand out clearly with a colour peculiar to the species.

Accessory sexual characters include ventral projections from both cardines and stipetets which appose each other on each side, like finger and thumb, (Figs. 30G. 34A, 38A) except in *Proteroiulus fuscus* (Figs. 33D, E) where only the cardines are produced. The first pair of legs in the male are modified into crochetiform organs but usually retain more evidence of their derivation from normal legs than those of julids. Most of the legs, except the hindermost pairs, carry one or two lanceolate setae on the post-femora and tibiae, sometimes on the femora also, these serve a function analogous to the adhesive pads on the legs of julid males.

The gonopods stand proud of the seventh ring and are not retractable into the lumen of the ring; they lie posteriorly along the trunk beween leg pairs 10, 11 and 12. The anterior protective peltogonopods still retain single jointed remains of the telopods lateral to the median coxal processes, but the posterior gonopods bear less evidence of their derivation from normal ambulatory limbs; they are long and slender rami with little, if any, coxal base and very reduced sternal component. The vulvae have diagnostic value when males are not available. The vulval sacs are much longer than those of a julid.

One of our species, *Proteroiulus fuscus* is parthenogenetic in Britain; *Archiboreoiulus pallidus* is normally sexual but Palmen (1949) reports that it is parthenogenetic in parts of its range.

Key to British species of Blaniulidae

1. With ocelli **2**

Without ocelli and without pigment, but coloured contents of ozadenes contrasting **5**

2. Ocelli in very acute triangular field consisting of an antero-posterior line augmented by two or three ocelli forming an additional line close to the base of the antenna (Fig. 30C, D) .... *Proteroiulus fuscus* (older stadia) (p. 107)

Ocelli in a single antero-posterior line (Fig. 30E, F, G) **3**

3. Moderately to well pigmented, amber to brown colour **4**

Lightly pigmented, cream-white colour .... *Nopoiulus kochii* (p. 113)

4. Fewer than ten setae fringing metazonites (Fig. 30E, F) .... *Proteroiulus fuscus* (younger stadia) (p. 107)

More than ten setae fringing metazonites (Fig. 30G) .... *Choneiulus palmatus* (p. 110)

5. Setae fringing metazonites long and prominent (Figs. 36A, 37A); adults usually longer than 10 mm and broader than 0.4 mm **6**

Setae fringing metazonites very short and difficult to see. Adults usually shorter than 10 mm and thinner than 0.4 mm in diameter (Fig. 38) .... *Boreoiulus tenuis* (p. 120)

6. Fringing setae about one quarter the length of metazonite (the wider part of the ring); ozadenes blood-red in life, darkening in preserved animals and sometimes staining much of the surrounding cuticle; gonopods and vulvae as in Fig. 36 .... *Blaniulus guttulatus* (p. 116)

Fringing setae nearly half the length of the metazonite; Ozadenes light brown to orange in freshly killed and recently preserved animals (much ligher in older material); gonopods and vulvae as in Fig. 37 ....*Archiboreoiulus pallidus* (p. 118)

Proteroiulus fuscus (Am Stein)
(Fig. 33)

Blaniulus fuscus Am Stein, 1857: *Jahresber. Naturf. Ges. Graubunden*, N.F. *2*: 139

Male	VI–VII	24, 27–29(34)	Length: 6.5–8.5 mm	Diameter: 0.5–0.7 mm
Intercalary male		31		
Female	VII–XIV	26–40(42)	7.0–13.4(15)	0.5–0.9

Brown to dark brown with ozadenes an even darker brown. 6 to 14 setae just longer than the metazonite (slightly shorter and fewer than in *Choneiulus palmatus*).

Ocelli in younger stadia in a single line as in *C. palmatus*, usually one fewer ocelli than the stadium number. By stadium VIII there are 7+ ocelli and one or two of the most anterior are displaced anteriorly (upwards) from the line.

Biology. Males of this species are rare (but perhaps not quite so rare as in *Nemasoma varicorne*). Brookes (1963) records six mature males and an intercalary amongst his collections of several thousand individuals. Recently I picked up a mature male and 4 females in a Perthshire birch wood; Dr. Gabbutt brought me 20 females and 2 males from Silwood Park, Berkshire. However, finding a male is still an occasion of some note. Rantala (1970, 1974) established that the species is parthenogenetic; unfertilized eggs usually develop into females but occasionally into males, especially in culture. Verhoeff (1933, 1939) had a high proportion of males in material from the Tyrol which he cultured. Brookes (1963, 1974) is of the opinion that the occurrence of males might be due to ideal conditions of culture and does not support Verhoeff's suggestion that there may be a bisexual race in Italy. Enghoff (1978b) found no spermatozoa in the seminal receptacles of the females collected in the presence of males. Curiously, the males which do occur exhibit periodomorphosis and Rantala (1974) reared a male through six successive intercalary stadia, a copulatory and two further intercalaries over a period of 6 years.

Brookes (1963, 1974) has given details of the anamorphosis and life-history of populations in a Cheshire wood. Eggs are laid from May to July in small clusters. In a plantation of larch and spruce they developed mainly to stadium II for the first winter, V for the second and VII for the third; on a nearby site with felled elms receiving more sunlight the population reached stadia III, VI and VIII by the first, second and third winters respectively. Females first matured at stadium VII; there is thus a period of three years beween generations.

Distribution

British Isles: First recorded by Pocock (1893) from Ireland. In 1972 it was the eighth commonest species; it is now the sixth commonest. There are records for 92 of the 112 vice-counties of Britain and from 25 of the 40 Irish. Found typically under the bark of fallen logs and stumps of both coniferous and deciduous trees; with *Cylindroiulus punctatus* it is the commonest sub-cortical species. Sometimes associated with the less common *C. britannicus* and *Nemasoma varicorne*. The species is sometimes found in well established populations within leaf litter and soil.

Europe: Found throughout Europe from Central Italy in the south, Finland in the north, and as far east as Bulgaria and the European plain of the Soviet Union.

An account of the ecology of this species in Finland is given by Peitsalmi (1981). Also introduced into Nova Scotia, eastern USA, South Africa, the Azores, Madeira and St. Helena.

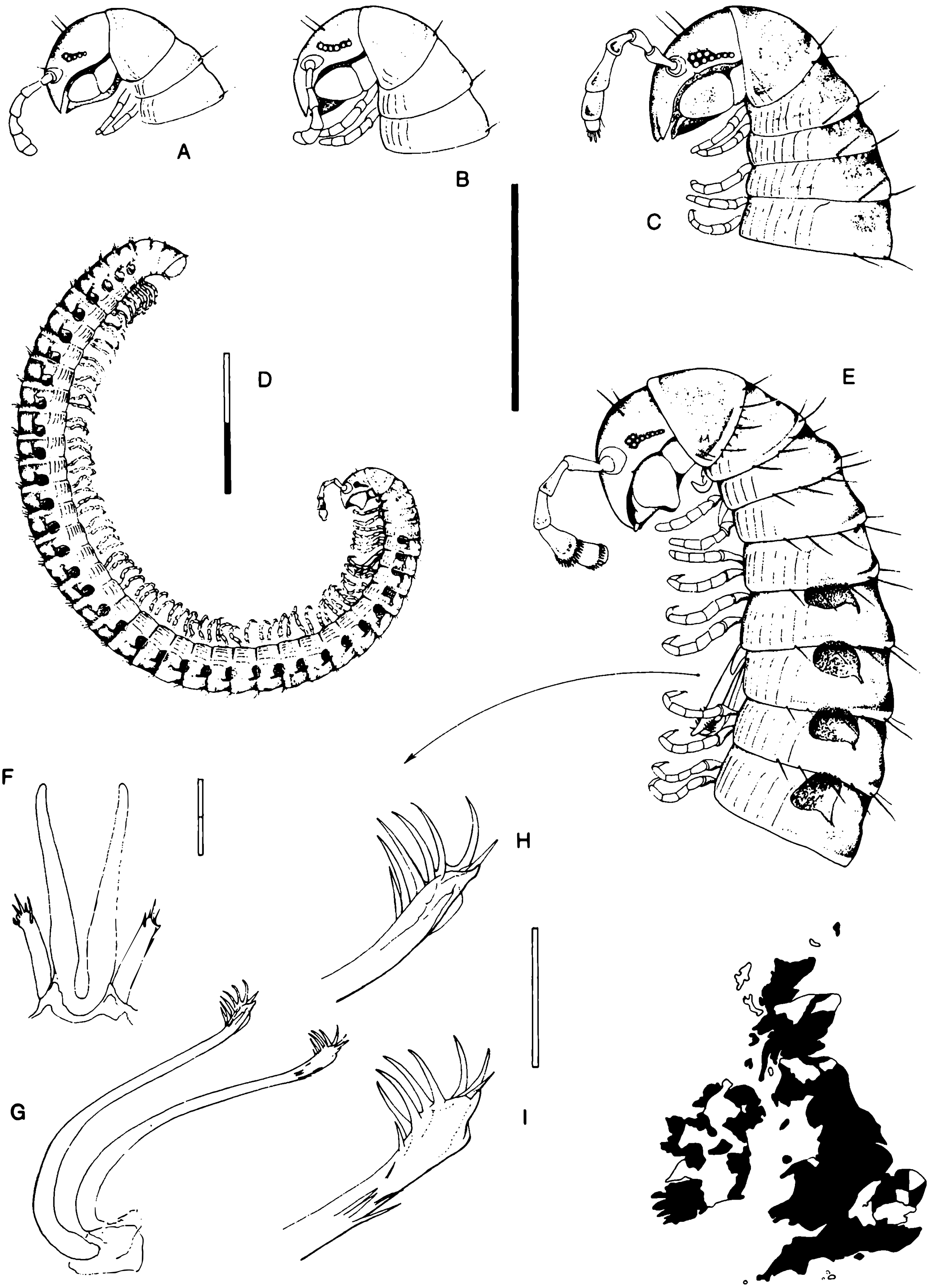


Fig. 33. ***Proteroiulus fuscus.*** A. A juvenile at stadium VI with 5 ocelli; B. A juvenile at stadium VII with 6 ocelli; C. An adult female, stadium X(?) with nine ocelli; D. An adult male, stadium XI(?) with nine ocelli; E. Enlarged view of the head and rings I to IX of the same male as in D, showing the expanded stipes, the crochet-form first pair of legs and the gonopods on ring VII; F. The peltogonopods (limb pair 8); G. The gonopods in anterolateral view; H. Apex of the right gonopod, external profile; I. Apex of left gonopod, internal profile.

Choneiulus palmatus (Nemec)
(Fig. 34)

Blaniulus palmatus Nemec, 1895: *Sitz. Ber. Bohm. Ges. Wiss. 1895*(2)
Nr. 38, 5–6, pl. 1, Figs. 7–11

Male	VIII	(25) 32 (56)	Length: 5–15 mm	Diameter: 0.3–0.5 mm
Female		(25) 31–32 (41)	6–12	0.4–0.6

Greyish brown with very dark brown, almost black ozadenes; immature individuals much lighter; there is a whorl of 14–20 setae fringing the metazonites; the setae are longer than the length of the metazonite. Ocelli are arranged in a single antero-posterior line parallel to the ventral edge of the head capsule; up to stadium VII there is one fewer ocelli in the line than the stadium number and in this respect the arrangement is indistinguishable from that of *Proteroiulus fuscus* (p. 107). In the first adult stadium, VIII, there are seven ocelli in the line. Adults of *P. fuscus* can be distinguished by one or two ocelli being displaced anteriorly and upwards from the line.

The very conspicuous numerous and long metazonite setae contrast with those of *Proteroiulus fuscus* and *Nopoiulus kochii.* (p. 113). In *P. fuscus* there are only 12–14 setae of medium length (about equal in length to the metazonite); in *N. kochii* there are about ten setae of similar length to those of *P. fuscus*.

Distribution

British Isles: Probably first recorded as British by Bagnall (1912b) from Gibside and Fencehouses, Durham and Harbottle in Northumberland, and in the next year, from the Botanic Garden, Glasgow. Bagnall (1912b, 1913b) initially referred his finds to *Blaniulus pulchellus* C. L. Koch, but later (1917b) to *Nopoiulus palmatus* in view of remarks by Brade-Birks of the same year. Jackson (1914) recorded animals from nursery gardens near Chester, and later (1916) from a greenhouse at Whalley Range, Manchester, as *B. pulchellus.* Brade-Birks (1917b) referred Jackson's materials to *N. palmatus* and I have reexamined the material and confirm that it belongs to the species now called *Choneiulus palmatus*.

Johnson (1913, 1915), Selbie (1913) and Foster (1919) all recorded *B. pulchellus* from Northern Ireland but Dr. Enghoff has examined the specimens in the Dublin Museum listed by Petersen (1975) and found them all to belong to *Proteroiulus fuscus.* Brade-Birks (1917b) and Jackson (1916) both refer to material of both sexes collected by Foster in Northern Ireland and this was probably *C. palmatus.* However, the occurrence of this species in Northern Ireland cannot be certain until valid specimens are available (see also remarks under *N. kochii*), however, there is a recent record from Kildare (H19).

Brade-Birks (1917) had the species from the Tivoli Gardens at St. Leonards in Sussex and this was the first southern record. I have had the species from

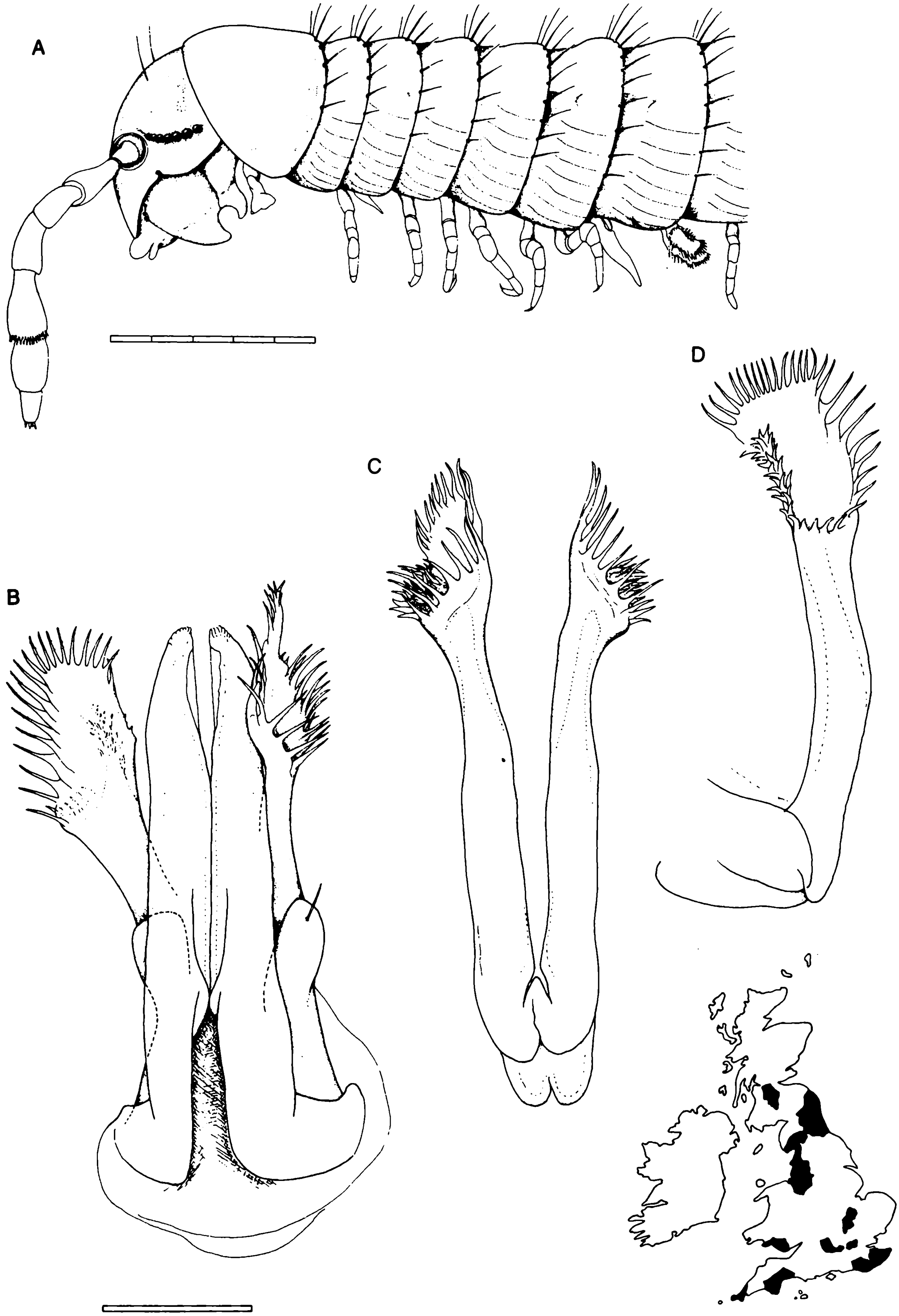


Fig. 34. *Choneiulus palmatus*. A. Head and rings I to VIII of a mature male; B. Gonopod complex in ventro-anterior view, slightly from the right. Note the difference in the appearance of right and left gonopods with only this slight difference of aspect; C. Gonopods in anterior view; D. Left gonopod, external profile.

a greenhouse at the Merlewood Research Station of the Institute of Terrestrial Ecology, 1954, and from an outdoor site at Compstall in Cheshire, 1958. More recently Mr. H. Williams found young and adults in tunnels beneath an old mill in Stockport, Cheshire. Dr. R. C. Welch recorded the species from Monk's Wood National Nature Reserve, Hunts (VC31) in corrugated paper bands around oaks, 1969. Also from South Devon (VC3), Blean, East Kent (VC15), J. Anderson, 9/72 (pers. com.) and perhaps from Wytham Wood, Berkshire (VC22), recorded as *N. minutus* (K. Southern, pers. com.). Dr. A. J. Rundle sent to me a stadium V individual from Kew, probably of this species. The species has been collected from a small isolated garden off Tavistock Place, St. Pancras, London (VC21) (Davis, 1979).

Europe: France, Germany, Switzerland (synanthropic), Belgium, Holland (Botanic Garden and from mole's nest), Sweden (mostly synanthropic but also in open habitats near the west coast), Denmark (synanthropic), S. Norway and Finland (greenhouses), USSR (greenhouses), Poland (synanthropic), Czechoslovakia, Hungary and Italy.

Also introduced into Nova Scotia and Madeira.

Nopoiulus kochii (Gervais)
(Fig. 35)

Iulus kochii Gervais, 1847: Myriapodes in: Walckenaer, *Histoire Naturelle des Insectes* (replacement name for *I. pulchellus* C. L. Koch, 1838).

Nopoiulus minutus (Brandt, 1841) of Brade-Birks (1939) and Blower (1958) but incorrect synonomy.

Nopoiulus venustus (Meinert, 1868) ex parte, in the sense of Schubart (1934).

Blower (1958) gives records for this species, as *N. minutus*, by Bagnall from Durham, Northumberland and Glasgow, by Jackson from Lancashire and Cheshire and by Johnson, Selbie and Foster from Ireland, mostly Ulster. All these records were made during the period 1911–1919 under the names of *Blaniulus pulchellus* C. L. Koch or Leach. Koch's species was recognized as a synonym of *Blaniulus venustus* Meinert but Leach's species was a synonym of *B. guttulatus* (Bosc). Bagnall gave Koch as the authority and latterly always quoted *venustus* as a synonym, whereas the Irish recorders gave Leach as their authority.

The animals from Durham which Bagnall (1912b) referred to *B. pulchellus* were later recognized as *Choneiulus palmatus* (see Bagnall, 1917). Bagnall (1917) refers to Brade-Birks (1917b) who tentatively reattributed the record of *Nopoiulus pulchellus* from a Manchester Greenhouse (Jackson, 1914), to *Nopoiulus palmatus.* In the same paper, Brade-Birks said that Brolemann had confirmed Irish specimens as *N. pulchellus* Leach, but Brolemann was probably referring to what is now called *B. guttulatus.* The curious result of this confusion was that Bagnall (1918) and Brade-Birks (1934, 1939) included both *N. pulchellus* (= *venustus* Meinert) and *N. palmatus* Nemec in their check-lists, notwithstanding that all the specimens they had handled of the former had all turned out to be the latter.

Recently Enghoff (private communication) has examined the material in the Dublin Museum listed as *venustus* in Petersen's list (1975) and found that all were *Proteroiulus fuscus.* Indeed, many of Johnsons specimens came from under bark whereas both *Nopoiulus venustus* and *Choneiulus palmatus* are usually found in hothouses. I have examined the material from the Manchester greenhouse to which Jackson gave the name *venustus* and confirm that they are all *C. palmatus.*

There remains no evidence that *N. minutus* (= *venustus* in the sense of Schubart, 1934) has ever occurred in Britain, but there is a possibility that it may occur.

But the matter does not end here. Brade-Birks (1922), *Notes on Myriapoda*, XXVI, keen to abandon the omnibus names *pulchellus* and *venustus* considered restoring either *minutus* Brandt or *kochii* Gervais, and since Chamberlin had regarded these as synonyms, he adopted the earlier name *minutus*. Enghoff & Shelley (1979) examined Brandt's type of *minutus* and found that it was not the species recorded throughout Europe as *venustus* (in the sense of Latzel, 1884 or Schubart, 1934). They therefore readopted the name *kochii* of Gervais. Enghoff & Shelley found Brandt's *minutus* to accord with an undescribed American parthenogenetic species which has not yet been found in Europe.

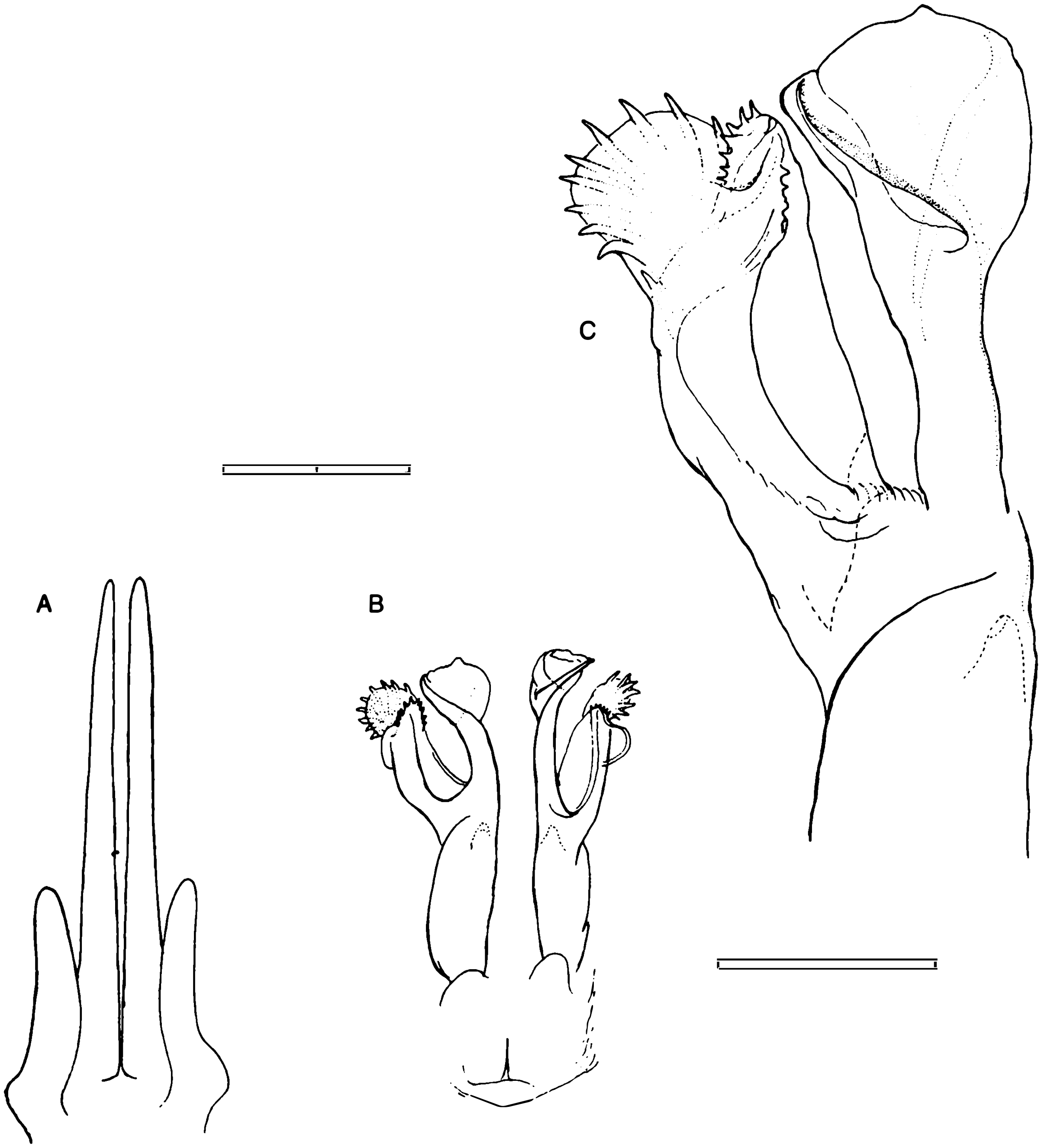


Fig. 35. *Nopoiulus kochii.* A. Peltogonopods (leg pair 8); B. Gonopods (leg pair 9); C. Apex of gonopod enlarged.

Blaniulus guttulatus (Fabricius)
(Fig. 36)

Julus guttulatus Fabricius, 1798: *Supplementum Entomologiae Systematicae*: 289

Blaniulus guttulatus (Bosc) of Blower (1958) & authors until Hoffman, 1979

Male	VIII	33–46(47)	Length: 8–12(14 mm)	Diameter: 0.4(0.6) mm
Female	IX–XI	36–46(54)	(9)12–15(16)	0.5(0.7)

Whitish to cream with bright deep blood red ozadenes (in *Archiboreoiulus pallidus* (p. 118), a blind blaniulid similar in many respects to *Blaniulus guttulatus*, the ozadenes are orange to orange yellow). In alcohol, the ozadene secretion sometimes discharges and stains the whole integument. There is a conspicuous fringe of metazonite setae, slightly shorter than those of *A. pallidus* (see Fig. 37). This is the common spotted snake millipede often encountered in gardens and arable land where it has long been recognized as a hazard to seedlings. (See Cloudsley-Thompson, 1950).

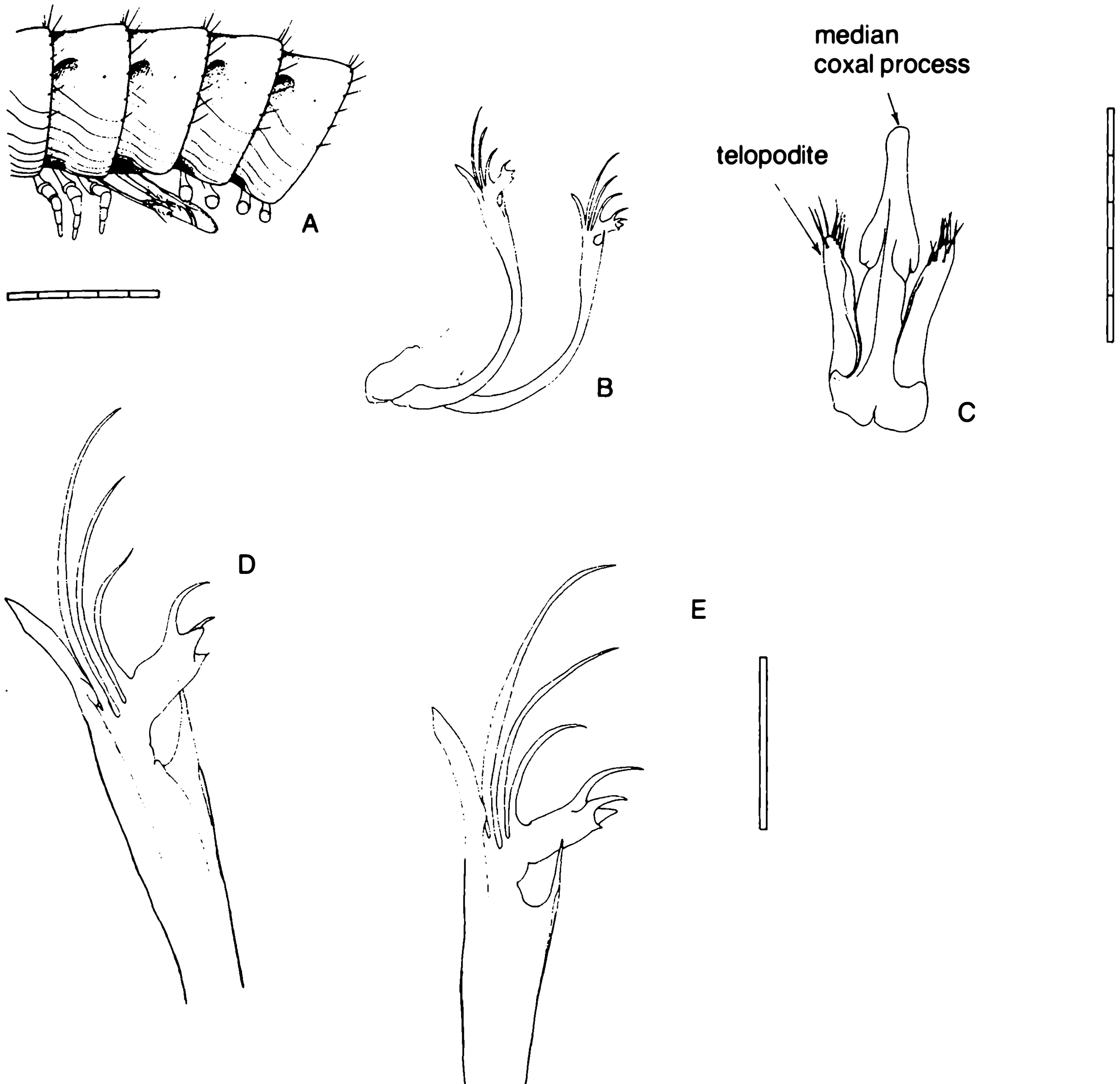
Biology. The depredations of this and other blind blaniulids on the sugar beet crop and others has recently been the subject of intensive investigations at the Institute Agronomique, Gembloux, in Belgium (see Biernaux, 1972). Baker (1974) reported on the economics of the species in Britain. Kinkel (1955) gives details of reproductive biology; Biernaux (1972) describes anamorphosis; Brookes (1963) gives details of early anamorphosis and Brookes & Willoughby (1978) describe the life cycle of a mid Wales population: the species spends three years as immature stadia overwintering as II(III), IV(V) and VI(VII), finally maturing in their fourth year at stadium VIII (males) and IX (females). Blower (1979) found a similar pattern of overwintering with the emphasis on the earlier of the two alternative stadia given by Brookes & Willoughby, in a population in South Wales. This long period of development leads to a broadly based age structure. In south Wales only 3–9% of an overwintering population of 100–300 per square metre were adult.

Distribution

British Isles: First recorded by Leach (1815). It was numbered the tenth commonest species in Britain and Ireland in Blower (1972) and demoted to eleventh in the survey's 1980 list. Not recorded north of Perth, Fife and Argyll in Scotland. It is certainly the commonest blind julid in both woodland and open land, especially in good arable loams. It is not frequent in base deficient soils and is generally absent from sandy soils; in base rich, calcareous soils it is sometimes associated with *Archiboreoiulus pallidus* (p. 118) and *Boreoiulus tenuis* (p. 120).

Europe: Throughout the continent.

Introduced into Canada, USA, Madeira, Azores, Canaries, St. Helena and Tristan da Cunha.



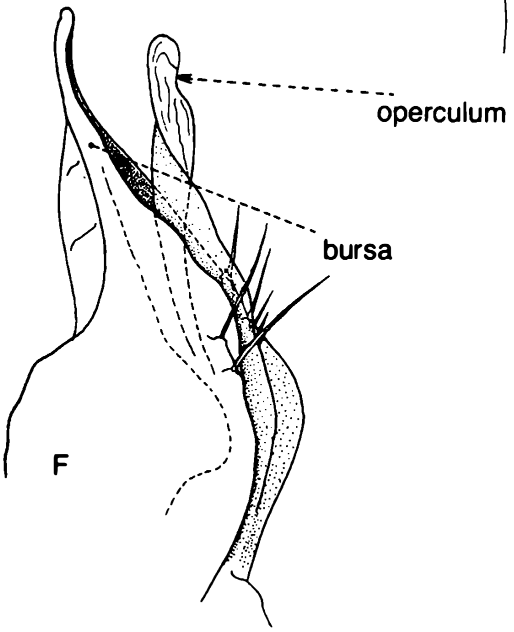


Fig. 36. ***Blaniulus guttulatus.*** A. Rings VI to IX showing metazonite setae and gonopods *in situ*; B. Gonopods in lateral view; C. Peltogonopods in posterolateral view; D. Apex of left gonopod, external profile; E. Apex of right gonopod, internal profile; F. Antero-internal view of vulva.

Archiboreoiulus pallidus (Brade-Birks)

(Fig. 37)

Proteroiulus pallidus Brade-Birks, 1920: *Ann. Mag. nat. Hist.*, (9) *6*: 364–365, Fig. 1

			Length:	Diameter:
Male	(VII?)VII–X(XI)	36–47	8.8 –14.6 mm	0.53 –0.68 mm
Female	IX–	(35)41–43(47)	(8.5)–12.3(15)	(0.37)–0.73 mm

Similar in size to *Blaniulus guttulatus* (p. 116), with a similar number of metazonite setae, but these are slightly longer than those of *Blaniulus*. (See Figs. 36 & 37). The colour of the ozadenes contrasts with those of *B. guttulatus*; they are paler orange to orange-yellow and do not discharge on fixation; thus alcohol specimens retain their natural light colour.

Distribution

British Isles: First recorded (and described) by Brade-Birks (1920b) from a runner bean plot at Wye College, East Kent (VC15). Secondly found by Morris (1922, 1927) in his survey of the faunas of Broad Balk fields at Rothamsted Experimental Station, Hertfordshire (VC20). Thirdly by Blower (1952) from the North Riding of Yorkshire (VC62). Ten additional vice-county records appear in Blower (1972) and a further eight in England and Wales, two in Ireland and one in Scotland have been added by the British Myriapod Survey.

A. pallidus occurs mainly in calcareous soils, sometimes associated with *Blaniulus guttulatus* and *Boreoiulus tenuis* (p. 120) and is implicated along with these in damage to sugar beet seedlings and other crops (see note under *B. guttulatus*).

Europe: There are occasional records of this species from Germany, Denmark, Belgium, Norway, Sweden, Finland and European USSR where the species is mainly synanthropic. According to Palmen (1949) the species is parthenogenetic in the northern part of its distribution.

Also from Canada, Ontario.

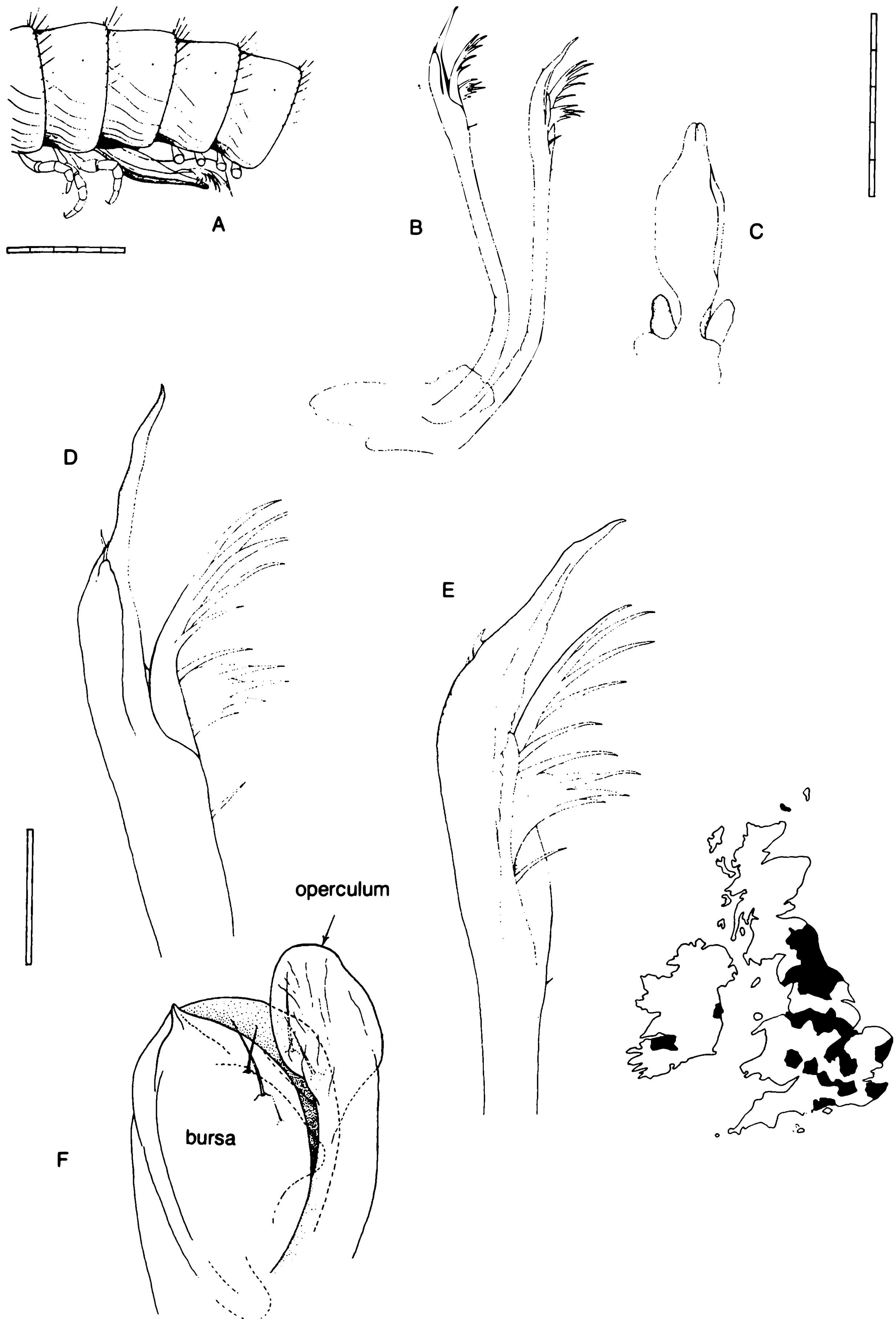


Fig. 37. *Archiboreoiulus pallidus.* A. Rings VI to IX showing metazonite setae, slightly longer than in *B. guttulatus* (Fig. 36), and gonopods *in situ*; B. Lateral view of gonopods; C. Anterolateral view of peltogonopods; D. Apex of left gonopod, external profile; E. Apex of right gonopod, internal profile; F. Antero-internal view of vulva.

Boreoiulus tenuis (Bigler)
(Fig. 38)

Monacobates tenuis Bigler, 1913: *Rev. Suisse Zool.*, *21*, 750–752

		Length:	Diameter:
Males VII–XII, (incl. calaries)	(29)31–36(43*,48)	(6)7.1–8.3(8.5) mm	(0.32)–41 mm
Females VIII,	(29)35–36(48)	(6)7.4–8.7(11.0) mm	(0.34)–0.44(0.46) mm

This is the smallest of our blind blaniulids; indeed, it is the smallest European blaniulid and is slightly thinner than *Nemasoma varicorne* (p. 102). Cream white with orange to orange red ozadenes and thus very similar to *Archiboreoiulus pallidus* (p. 118) but quite distinctive in the apparent absence of metazonite setae which are very short and difficult to see.

B. tenuis is the only member of the Julida to add three rings at the moult from stadium I to stadium II. Stadium II thus has two ozadenes as opposed to the usual one and these first formed glands remain recognizable in later immature stadia. Males undergo periodomorphosis.

Distribution

British Isles: First recorded by Bagnall (1918) from two vice-counties in the south, five in the north and one in Scotland (Edinburgh). Seven further vice-counties were listed by Blower (1972) making a total of 15. Most recently the species has been found in Bedford (VC30) by Dr. Rundle (in five separate Km squares), Yorkshire (VC63) Cheviot (VC68) and in five Scottish and eight Irish vice-counties by the British Myriapod Survey. Now with 31 vice-counties, *B. tenuis* has just overtaken *A. pallidus* with 26 records and, unlike *pallidus* these include records in Scotland.

Occurs in woodland, especially in base rich soils and also in arable land associated with *B. guttulatus* (p. 116), for example, in sugar beet fields at high densitites.

Europe: There are scattered records from Holland, Belgium, France, Denmark, Norway, Sweden, Germany, Poland and European USSR.

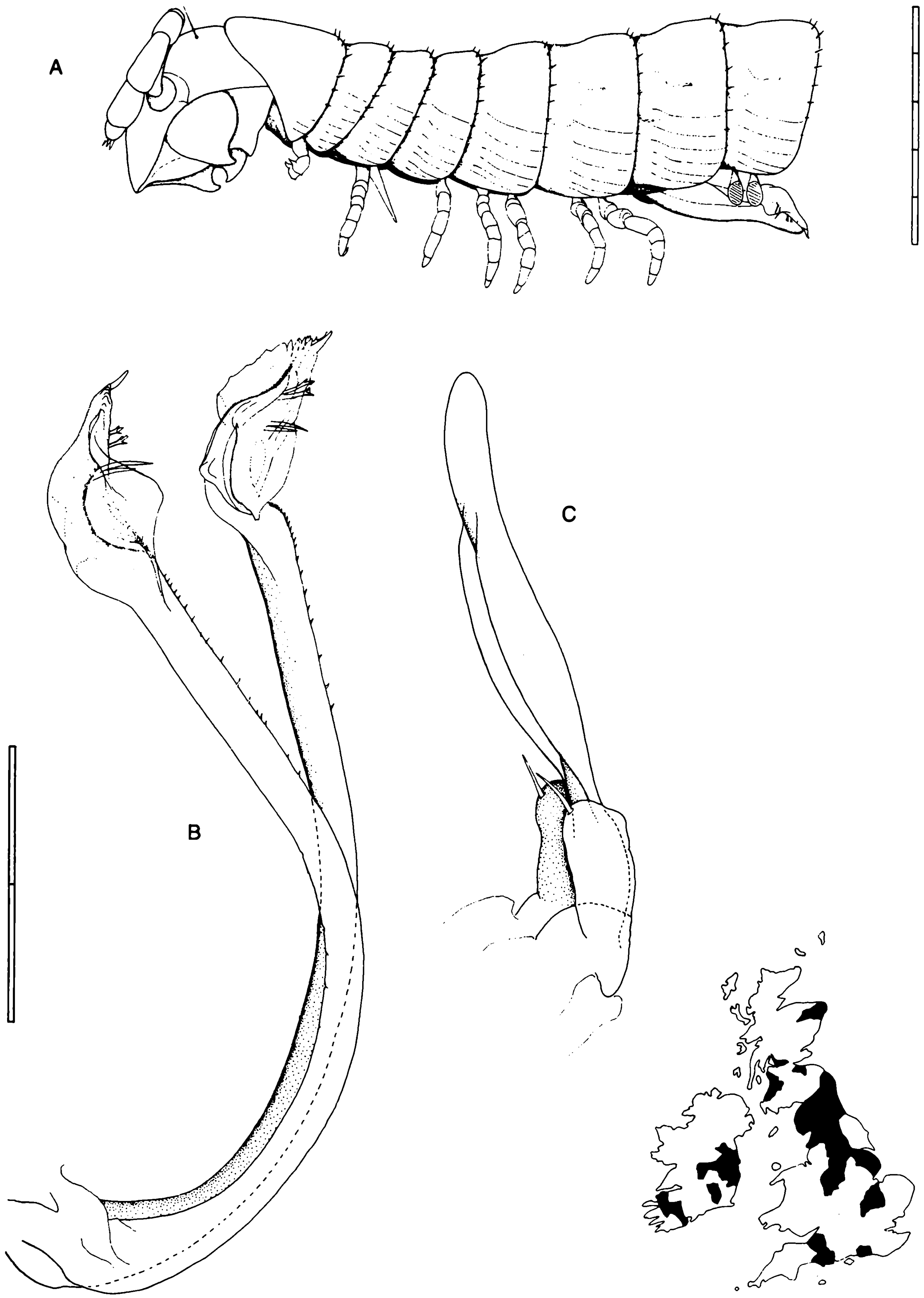


Fig. 38. *Boreoiulus tenuis*. A. Head and rings I to VIII of the mature male; note the very short metazonite setae; B. Gonopods in profile from the left side; C. Peltogonopods in profile from the left side showing mesal coxal process and lateral telopodites with a single apical seta.

Family JULIDAE

This is the largest family represented in Britain by 18 of our total of 52 species. It is therefore appropriate to recognize five groups of species which are here given the status of tribes. In other systems they are considered as subfamilies or even separate families; they are held at low rank in this *Synopsis* to indicate the unsettled state of the suprageneric categories. The tribes are partly recognizable by their somatic characters, but final placement depends, as usual, on the secondary sexual characters especially the gonopods. The key which follows includes bifurcations which do not wholly correspond to the tribal boundaries because it utilizes easily discernible characters such as presence or absence of eyes and caudal projections, which are derived characters.

The family includes a range of small, medium and also the largest snake millipedes in Britain. Julids are stockier than the other two families of julidans; males have a length:diameter ratio of 10–14:1; females are invariably stockier. The length:diameter ratio of blaniulids and nemasomatids ranges from 20:1 to 30:1. The exceptions are the blaniulid *Proteroiulus fuscus* (p. 107) which could almost pass as a julid with a ratio of 12–15:1, and the julid *Leptoiulus kervillei* (p. 178) small males of which are almost blaniulid-like with a length: breadth ratio of 20:1.

Somatic characters

Julids are generally well-pigmented and the contents of the ozadenes are only easily visible in less-pigmented younger stadia. The darker species are, usually, but not invariably, the larger. The prozonite is separated from the metazonite by a distinct suture; longitudinal striae or flutings extend all round the ring. A whorl of setae may fringe the posterior edge of the ring; the setae are very much reduced or absent in the Schizophyllini and in most Cylindroiulini. The pre-anal ring is often produced median dorsally into a caudal projection or tail (Figs. 39, 40).

Secondary sexual characters – Pairing equipment

Males are provided with structures to facilitate close union with the female during pairing. The first pair of legs are profoundly modified into a pair of hooks or crochets which locate beneath the head capsule of the female. *Julus scandinavius* (p. 168) does not have this pair of crochets and the location of the anterior ends is dependent on a pair of coxal projections from the second pair of legs of the male which the female grasps with her jaws. Of the cheek lobes, only the cardines are expanded in the julids, not both cardines and stipetes as in most blaniulids. There are no expansions from the cheek lobes in male Julini. Securing a firm hold on the female is helped by adhesive pads ('sole-pads'), on the postfemora and tibiae of most leg pairs, declining or disappearing towards the end of the trunk. These 'sole-pads' are absent from our British species of Julini where males do not attempt the initial balancing act of mounting the smooth back of the female (see p. 168).

Gonopods

Gonopods are the modified limbs (8 and 9) of ring VII; as in blaniulids the anterior pair are the protective peltogonopods which shield the sperm-carrying posterior pair or gonopods proper. Unlike the blaniulids, julids carry their gonopods fully retracted within the lumen of ring VII where a gap is present in the normal sequence of legs. During pairing (or in preparation for moulting) the gonopods are everted on the crest of the gonopodal sac. In *Brachyiulus pusillus* (p. 183) the gonopods remain partly protruding when at rest.

Anterior parts

The peltogonopods differ from those of the Blaniulidae and Nemasomatidae in the complete absence of a rudiment of the telopodite, and in the frequent association with them of a component of the posterior pair of limbs to form a pair of pincers which help the female evert her vulvae during pairing. These apposed parts, the peltogonopods and the derivative from the ninth pair of limbs are called the *promerite* and the *mesomerite* respectively; the remainder of the gonopod proper which derives from the ninth pair of limbs is called the *opisthomerite* (see Fig. 13). In *B. pusillus* and *Julus scandinavius* the mesomerite is not apposed to the promerite in the manner described but remains in relation to the opisthomerite (Figs. 53, 58).

Posterior parts

The opisthomerite consists of an elaborate tubular structure or *solenomerite* arising from a coxal base with or without attendant coxal processes. This is the part of the gonopod directly involved in transferring sperm from the male opening to that of the female. A sperm canal runs along the solenomerite to open apically; parallel to this there is often a groove to guide the **flagellum**. This flagellum arises from the base of the promerite on its mesial side and passes towards the solenomerite where it is guided into its groove by a special flap at the base (e.g. Figs. 44E, 47D). In the tribes Schizophyllini and the Metaiulini there is no flagellum nor is there a groove for same. Within the tribe Cylindroiulini the flagellum is absent in the genus *Enantiulus* (p. 164).

The apex of the solenomerite may be flanked by a protective leaf-like lobe on its outer posterior aspect, the **phylacum** (well-developed in *Ophyiulus* and *Leptoiulus* (Figs. 54–56)). An anterior lobe, the **brachit** (in Cylindroiulini) or the **velum** (in Julini), and projections from the coxal base add to the complexity of the opisthomerite.

Examination

The detailed structure of the opisthomerite is absolutely specific, especially when examined in mesial profile. First dissect out the entire gonopod ensemble from ring VII; insert a needle mesially from the apical aspect and open the two sides about their basal connections like the leaves of a book to reveal their internal faces.

Succession of male stadia

In the stadium but one before that in which the male matures, the seventh ring loses its normal two pairs of limbs and gonopod rudiments appear in their place (Fig. 13). The first pair of legs remain in the normal condition; the two stadia with gonopod rudiments are termed larval males. In the Schizophyllini a mature male can moult into an *intercalary* stage with partial regression towards the condition of the larval male. In this intercalary stage the first pair of legs are somewhat intermediate between normal ambulatory and crochet-form and the cardine lobes are reduced, but not quite to their condition in the larval male (Fig. 12). The intercalary stage may become a second copulatory stage or another intercalary (see Fig. 12). In the Julini and most Cylindroiulini the mature male does not moult again. In *Cylindroiulus nitidus* mature males can moult directly into a second copulatory stage; intercalaries do not often occur.

The female characters

The vulvae lying behind the second pair of legs may assist diagnosis of females in the absence of males.

Examination

In order to extract the vulvae, first ease the head and the first pair of legs forwards, then chip-away the ventral tips of the pleurotergal tips of ring II to allow the second pair of legs to be eased forwards; ascertain that the vulval pouches at the base are intact, still attached, and ensure these are eased forwards along with the legs. At this stage it should be possible to detach the whole ensemble of the second pair of legs plus the vulvae in their pouches and mount, with posterior surface uppermost, in lactic acid or gum chloral. If necessary, one of the vulvae can be exposed further by dissecting away the posterior wall of the vulval sac.

Gynandromorphs

These occur from time to time. In my experience they are frequent in *Brachyiulus pusillus* (p. 183) and in laboratory reared *Ophyiulus pilosus* (p. 172); in these latter, close observation of individuals moulting through to adult reveals animals with both vulvae and gonopods because these structures are extruded just previous to the moult. Possibly the gynandromorphs are more frequent than realised; one does not naturally seek vulvae in what appear to be male individuals.

Parthenogenesis in not known to occur in any British species of julid.

Key to the British species of Julidae

1. With ocelli **2**
Without ocelli **18**

2. Telson produced as a pointed tail extending beyond the posterior level of the anal valves (Fig. 39) (the apex of this tail may be damaged in some animals) **3**
Telson either clubbed, or rounded and not obviously produced (Fig. 40), or, if pointed (*Brachyiulus*), not extending beyond the level of the anal valves. Only in one of the species with a clubbed tail does this extend nearly to the posterior level of the anal valves. Cylindroiulini (except *Cylindroiulus nitidus* and *Enantiulus armatus*) and Brachyiulini **10**

3. Apex of telson moderately produced, slightly or markedly upturned. Prozonites of older animals marked with fine transverse chasings. Adults well pigmented, brown-black (Fig. 39A, B) **4**
Apex of telson well produced, straight or slightly downturned (Fig. 39C). Prozonites quite smooth; setae fringing metazonites **5**

4. Telson markedly upturned; setae on tail grouped close to apex; no setae fringing metazonites; adults with dorso-lateral longitudinal stripes along the trunk (Fig. 41) .... *Ommatoiulus sabulosus* (p. 131)
Telson slightly upturned; setae on tail more evenly disposed along its length; with setae fringing the metazonites; adults nearly black with contrasting white legs (Fig. 42) .... *Tachypodoiulus niger* (p. 135)

5. Telson quite straight up to the hyaline apex which is slightly curved (concave side ventral); ozopores posterior to the suture between pro- and metazonites; adults moderately to well pigmented (Fig. 39C); tribe Julini, see Table 3 (p. 167) for more certain separation **6**
Telson slightly ventrally directed (Fig. 39D); ozopore *on* the suture between pro- and metazonite; adults lightly pigmented **9**

6. Adults lighter in colour, usually less than 1.0 mm in diameter (height); see Table 3 (p. 167) and Fig. 56 .... *Leptoiulus kervillei* (p. 178)
Adults darker in colour, usually greater than 1.0 mm in diameter (height) **7**

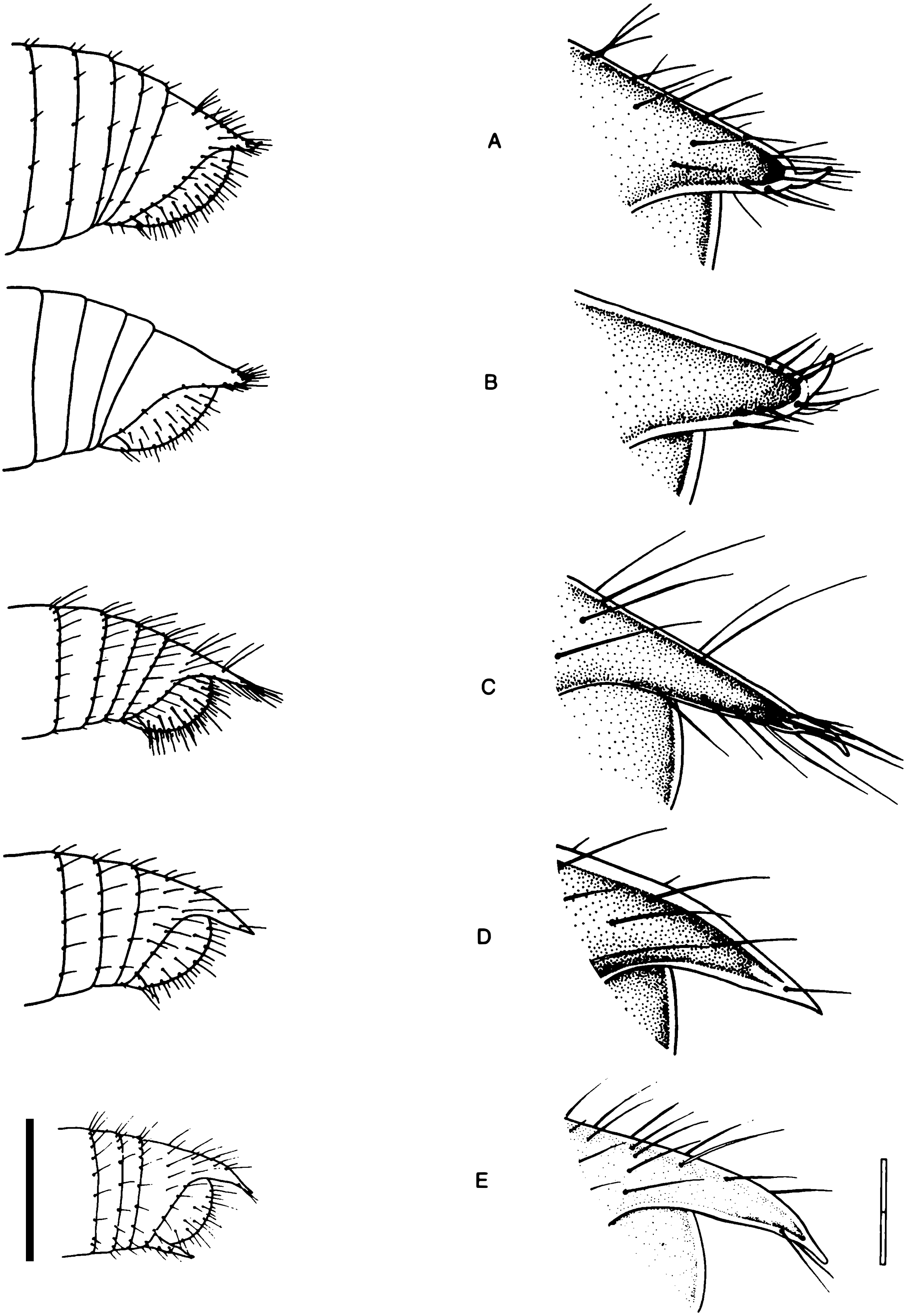


Fig. 39. Tails of British Julidae. I. Julids with pointed caudal projections. A. *Tachypodoiulus niger*; B. *Ommatoiulus sabulosus*; C. *Ophyiulus pilosus* (essentially simlar in *Julus scandinavius* and *Leptoiulus* spp.); D. *Cylindroiulus nitidus*; E. *Enantiulus armatus*. The right hand drawings show detail of the apex at higher magnification.

7. Adults with median dorsal lighter stripe; see Table 3 and Fig. 55 .... *Leptoiulus belgicus* (p. 176)

Adults black, brown-black or brown, without median dorsal lighter stripe **8**

8. Adults brown-black, mottled ventrally; metazonite setae very conspicuously long; see Table 3 and Figs. 1, 54 *Ophyiulus pilosus* (p. 172)

Adults an even oily brown; metazonite setae moderately long; see Table 3 (Fig. 53) .... *Julus scandinavius* (p. 168)

9. Sub-anal scale produced posteriorly almost as far back as the apex of the caudal projection (Fig. 52) .... *Enantiulus armatus* (p. 164)

Sub-anal scale not produced (Fig. 46) ...... *Cylindroiulus nitidus* (p. 150)

10. Sub-anal scale massive, projecting forwards under the last three rings (Figs. 40D, 59) .... *Unciger foetidus* (p. 186)

Sub-anal scale normal (Figs. 40A–C, F–I) **11**

11. Apex of telson distinctly club-shaped or smoothly rounded, not projecting. Metazonites without fringing setae (Fig. 40A–C, F, G, I) **12**

Apex of telson pointed, obtuse, roof-like, very slightly projecting over the anal valves. Small species, adults smaller than 14 mm long and 1.0 mm diameter. With two dorso-lateral yellow/cream bands extending along the length of the animal. Metazonites fringed with setae (Fig. 40H) .... *Brachyiulus pusillus* (p. 183)

12. Apex of telson distinctly clubbed (Fig. 40A, 40C) **13**

Apex of telson smoothly rounded, not produced (Fig. 40B, F, G, I) **14**

13. Apex of telson extending up to or slightly beyond the posterior limit of the anal valves (Fig. 40C). Adults up to 28 mm long, 2.1 mm diameter. Usually light brown in colour (Fig. 47) .... *Cylindroiulus punctatus* (p. 152)

Apex of telson not extending to the posterior limit of the anal valves (Fig. 40A); adults exceed 35 mm long and 3 mm diameter; adults usually quite black (Fig. 43) . *Cylindroiulus londinensis* (p. 140)

14. Larger and darker; adults usually longer than 19 mm, broader than 1.5 mm, shiny black (Fig. 44) ... *Cylindroiulus caeruleocinctus* (p. 144)

Smaller and lighter in colour (occasional older animals may be brown-black); adults rarely reaching 18 mm long and 1.4 mm broad . . . the *luscus*-group of *Cylindroiulus* **15**

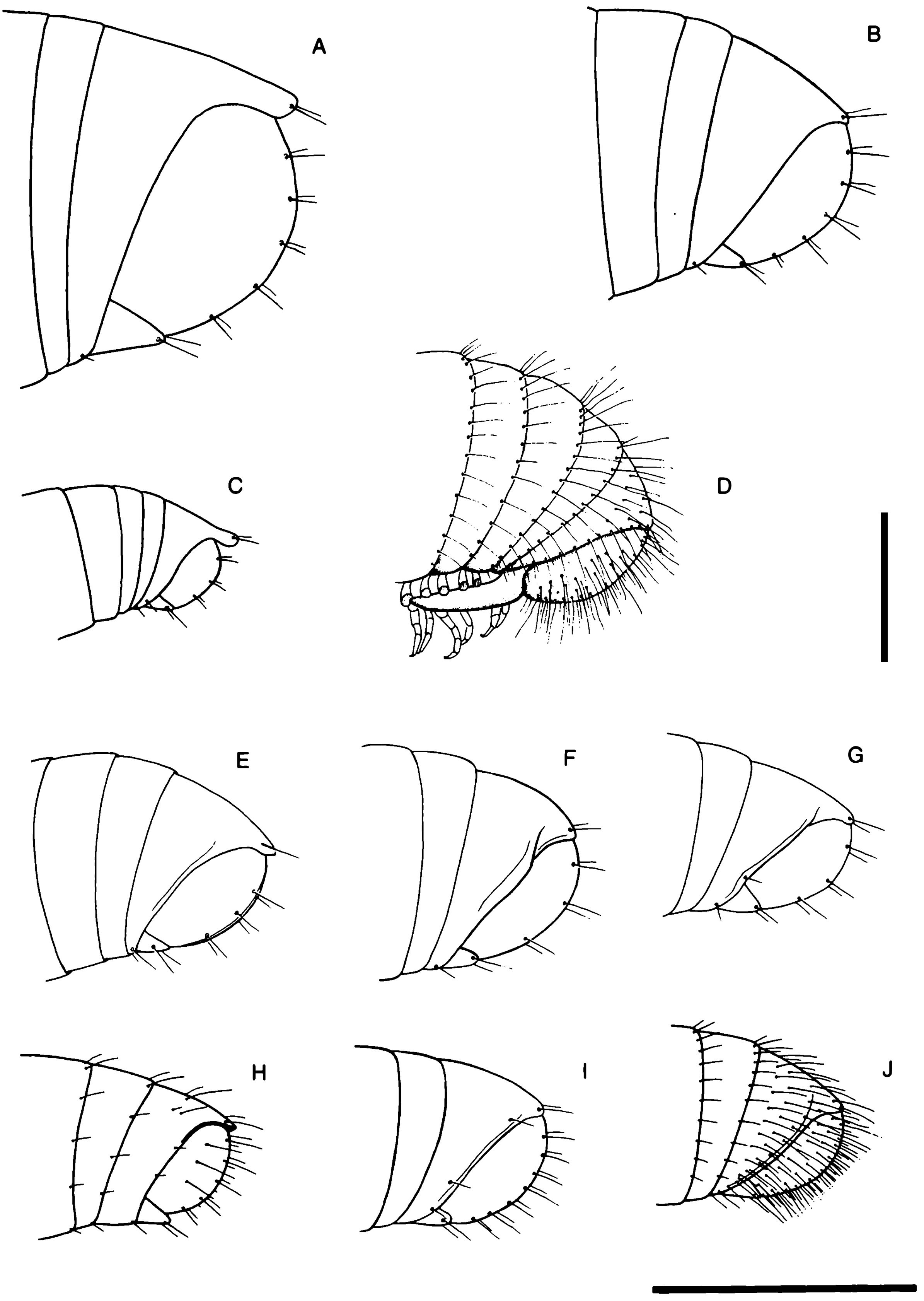


Fig. 40. Tails of British Julidae. II. Caudal processes not projecting beyond the posterior limit of the anal valves or absent. A. *Cylindroiulus londinensis*; B. *Cylindroiulus caeruleocinctus*; C. *Cylindoiulus punctatus*; D. *Unciger foetidus*; E. *Cylindroiulus vulnerarius*; F. *Cylindroiulus latestriatus*; G. *Cylindroiulus britannicus*; H. *Brachyiulus pusillus*; I. *Cylindroiulus parisiorum*; J. *Metaiulus pratensis*; Note the massive forwardly produced ventral scale in D, and the absence of metazonite setae in *Cylindroiulus* spp. A–C, E–G, and I.

15. With three setae on each anal valve (avoid counting setae on subanal scale) (Fig. 40G) **16**

With more than five setae on each anal value (Fig. 40I) **17**

16. Usually under bark and in dead wood (Fig. 49) but gonopods need checking .... *Cylindroiulus britannicus* (p. 158)

Halophile (coastal habitats) in sandy soil (Fig. 48) but gonopods need checking .... *Cylindroiulus latestriatus* (p. 155)

17. Usually under bark and in dead wood, rare. Males less than 10 × 0.75 mm, females less than 12.5 × 1.0 mm (Fig. 50) .... *Cylindroiulus parisiorum* (p. 160)

Males up to 10 × 0.8 mm, females 13 × 1.10 mm. Males sometimes with much more closely-set striae on metazonites. Found only in Kew Gardens (Fig. 51) .... *Cylindroiulus truncorum* (p. 162)

18. Telson produced as a pointed tail (Fig. 40E); very few setae on anal valves and none on the trunk; almost without pigment; tips of labrum, gnathochilarium and caudal projection amber coloured (Fig. 45) .... *Cylindroiulus vulnerarius* (p. 147)

Telson not produced; setae fringing metazonites; anal valves richly setose (Fig. 40J); lightly pigmented animals, confined to the south east, rare (Fig. 57) .... *Metaiulus pratensis* (p. 180)

Tribe SCHIZOPHYLLINI

Prozonites with rather irregular (*Ommatoiulus*) or regular (*Tachypodoiulus*) striations. Ozopore well posterior to the suture between pro- and metazonite. Caudal projection distinctly upturned. Both British species are heavily pigmented; in *T. niger*, contrasting white legs exaggerate the shiny black trunk and in *O. sabulosus* a striking pair of dorso-lateral orange stripes contrast with the otherwise darkly pigmented trunk. Both species have a wide horizontal and extensive vertical range and spend much time above ground climbing trees and walls. Although much of this activity is nocturnal, the striking coloration may conceivably be construed as aposematic. Both species are frequently seen in large numbers in unusual places such as on bare sandy shores or in and on buildings, sometimes on a scale which constitutes a nuisance to the occupants.

The gonopods of the two British species are without a flagellum and are otherwise highly distinctive. Males have expanded cardines and adhesive pads on the postfemora and tibiae (or just the tibiae) of the legs. Hoffman (1979) wonders whether *Tachypodoiulus* might not belong to the Cylindroiulini but it has been retained here in its more traditional position because of its close ecological similarity to *Ommatoiulus*.

Ommatoiulus sabulosus (Linné)
(Fig. 41)

Julus sabulosus Linné, 1758: *Syst. nat.* (ed. X), 1:640
Schizophyllum sabulosum, of Blower (1958) and of literature up to 1968
transferred to *Ommatoiulus* by Jeekel (1968)

Sexual dimorphism at stadium VI

Males	IX–XIV	40–52	Length: 14–23 mm	Diameter: 1.4–1.8 mm
Females	IX–XIV	40–52	19–33	1.6–2.8

Orange reddish rust brown or dark red brown, almost black pigment developed mainly in the two 60° dorso-lateral arcs beginning around the level of the ozadenes and in a median dorsal band. Thus a median-dorsal third of the upper hemicircle of each ring contains two lighter bands of straw-coloured to yellow pigmentation on either side of the median dorsal band which usually occupies about a quarter or less of the space between the lateral darkly pigmented areas. The overall appearance is of a dark orange brown dorsum decorated with two dorso-lateral orange-yellow bands crossing both pro- and metazonites.

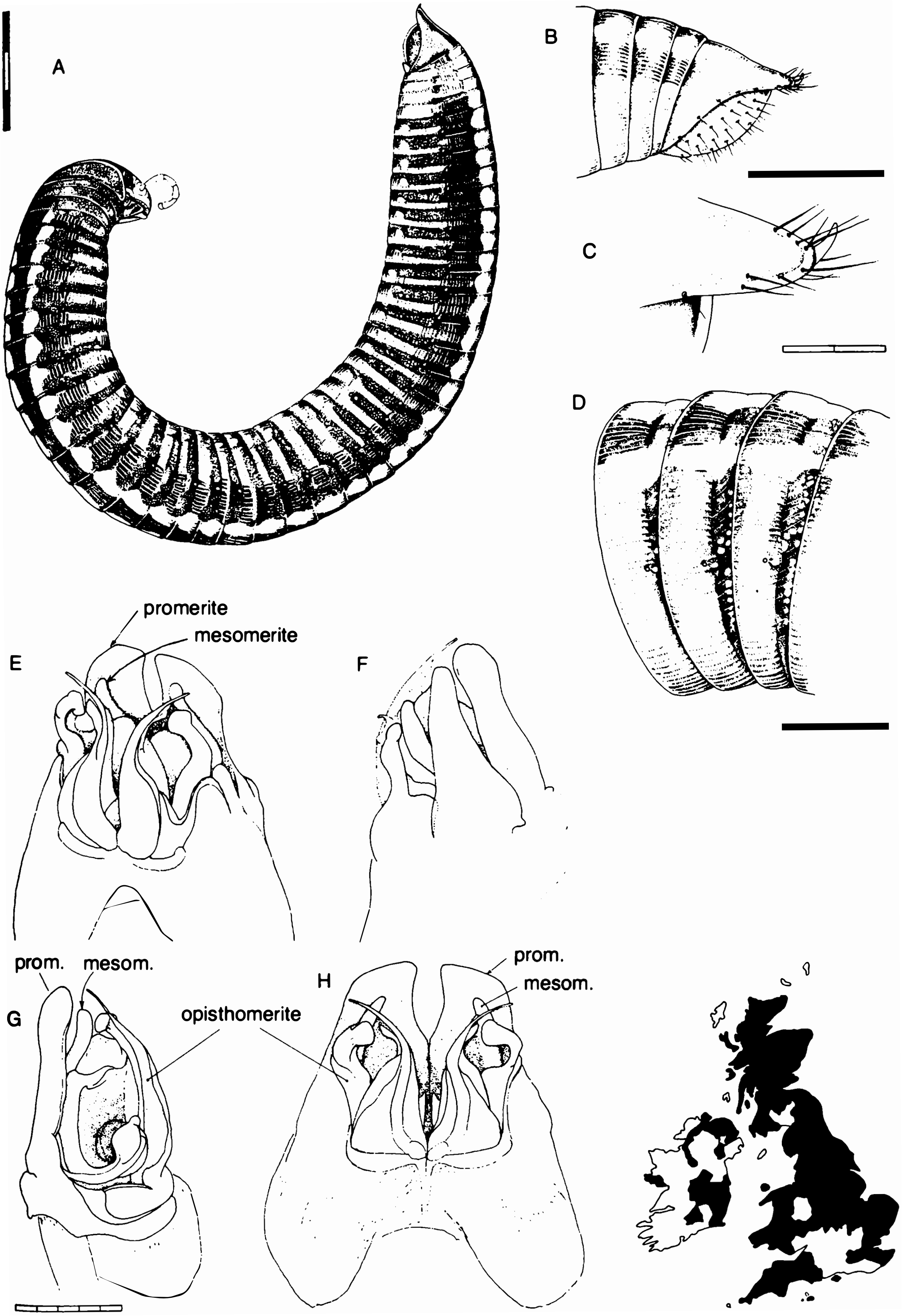
The usual variation is in the depth of the orange-brown pigment rather than in the pattern, but there also occurs a variation of pattern where the dorso-median pigmented band is expanded to occupy a third of the space between the lateral dark areas thus narrowing the light yellow bands; at the same time the darker pigment develops in the metazonites across the light bands and divides these into a series of yellow spots. These spots can be further restricted by an outward expansion of the dorso-median band anteriorly on each prozonite and an extension further dorsally of the lateral areas of dark pigment.

Therefore two forms are recognizable, one with continuous yellow-orange bands and one with two rows of dorsal segmental spots of yellow. I first encountered the maculate form at Whistman's Wood on Dartmoor over twenty years ago where the majority of individuals conformed to this pattern. Mr. Tremlett recently brought me some animals from this same wood and all were of the maculate form. I have seen the occasional maculate form from sites in Scotland, but never a pure population. The two forms may merge into a continuous series but it will be interesting to score future captures for pattern in a precise manner.

The prozonites are finely chased but in a less regular manner and the chasings are far less evident than those of *Tachypodoiulus niger* (p. 135). The metazonites are quite glabrous. The total absence of setae on the metazonites along with the aggregation of all telson setae at the apex of the projection helps to distinguish young stadia from those of *T. niger.* Immature stadia are much lighter in colour; there is just a small patch of pigment developed around the ozodenes and the median dorsal dark band is a very narrow line; these young stadia are less strikingly *Ommatoiulus*-like than the young of *T. niger* (stadia IV and V). As in *T. niger, O. sabulosus* has intercalary males which can be distinguished from ordinary males by smaller first legs than in the immature condition but not modified into the crochets of the mature condition.

Biology. Fairhurst (1968, 1974) gives details of the anamorphosis and life-cycle of populations living in sand dunes and adjacent conifer woods at Newborough in Anglesey. Animals born in summer spent the first winter as stadia IV and V and the second as VII, VIII and IX. In the dune area most males matured at stadium IX at two years old but in the forest males did not mature until stadium X after three years growth. Females in the dune area matured first at stadium X after three years but in the forest, at stadium XI after four years of growth. One or more stadia of intercalary males are interpolated between males in the copulatory condition; these are less active than mature males and are mostly found as overwintering animals.

Fig. 41. *Ommatoiulus sabulosus.* A. A female with 46 + 1 rings in lateral view, but twisted slightly to give a dorsolateral view of the anterior rings showing the dorso-median dark band and the two paramedian orange bands; metazonite setae are absent in this species. The white spots mid-laterally are the ducts leading to the ozopores (see enlarged view at D where both ducts and openings are visible); B. Tail end showing the upturned apex of the caudal projection; note the setae are confined to the apex (compare Fig. 42B, C); C. Enlargement of the apex of the caudal projection; D. Rings 17–20 to show oblique striae on the prozonites, ozopore posterior to the suture and the light ozadene duct leading to it; E–H. Gonopods. E, Posterior ventral view from the left; F, Antero-lateral view from the left; G, Inner profile of left gonopod; H, Posterior view.


A
B
C
D
promerite
mesomerite
E
F
prom.
mesom.
G
opisthomerite
H
prom.
mesom.

Distribution

British Isles: First recorded by Johnston (1835) from Scotland. Not so frequently recorded as *T. niger*; it is the ninth commonest species. *O. sabulosus* shows greater variation in its frequency of occurrence. It is ranked third in Scotland whereas Kime (1978) places it 23rd in his survey area of Surrey, west Sussex and Hampshire; he found it in only two of 137 Km squares in Surrey and not at all in Sussex and Hampshire.

It is absent from Wiltshire, and is very infrequent in Kent (Kime, pers. com.).

Like *T. niger, O. sabulosus* is a wandering species, extremely vagile moving over a wide range vertically and horizontally. It climbs trees and walls at night (it is occasionally beaten off trees by day). It is not so often recorded entering houses and other domestic areas as is *T. niger.* It is more characteristic of duneland and is often seen in large numbers on the foreshore adjacent duneland as, for example, on the Lancashire coast at Ainsdale, Newborough Warren, Anglesey and west Gower in South Wales. Inland it is associated with sandy soils (hence the trivial name) and coniferous woodland and heathland. It is thus the natural complement of *T. niger* which has a preference for limestone areas. However, like its fellow schizophylline it is so vagile that it can occur in almost any type of habitat. In a Gower limestone wood it is present along with *T. niger*, in some years more numerous, in others less numerous.

Europe: Although *O. sabulosus* is the less frequently recorded of our two schizophyllines and has the more restricted range in Britain, it has by far the wider distribution on the continent: Norway, Sweden, Finland, Esthonia, Lithuania, Denmark, Holland, Belgium, France, Germany, Poland, Czechoslovakia, Switzerland, Austria, Hungary, Bulgaria, Romania, USSR (European plain and Carpathians), Spain, Italy and Yugoslavia.

The general biology of the species has been studied extensively in Europe; Halkka (1958), in Finland was the first to elucidate details of anamorphosis. Sahli (see 1969b) has worked mainly on German material. Biernaux (1969) gives biological and distributional data for Belgium.

Tachypodoiulus niger (Leach)
(Figs. 5, 7, 12 and 42)

Julus niger Leach, 1815: *Trans. Linn. Soc. London, 11* (2): 378
Julus albipes C. L. Koch, 1838
T. albipes of continental authors

Sexual dimorphism at stadium VI

			Length	Diameter
Male	VIII–XIII	(38)39–50	15–35 mm	1.4–2.3 mm
Intercalary male	IX–XI	42–47	20–29	1.8–2.3
Female	VIII–XII	(38)39–49	17–39	1.6–2.9

Females exceptionally up to stadium XV (48 + 2, 44 × 3.5 mm)

Dark brown to almost black; the impression in life is of a black trunk with contrasting white legs. Air beneath the overlapping posterior parts of the metazonites sometimes gives the appearance of silver rings around each segment. Prozonites with fine transverse chasings which loop posteriorly at their lateral or ventro-lateral extremities; these chasings are best seen dorsally in a flexed portion of the trunk. Setae fringing the metazonites short, from a half to a quarter the length of the metazonite.

Immature stadia lighter brown; stadia IV and V with heavier pigment in two bands at the level of the ozodenes and in a median dorsal dark line. The two dorso-lateral lighter areas remaining give the animals a superficial resemblance to *Ommatoiulus sabulosus* (p. 131) or *Brachyiulus pusillus* (p. 183); adults of this latter species are about the same size as stadia IV and V. Stadium VI still lighter but without such a distinct pattern; stadium VII can be quite black and is the first to show the prozonite chasings clearly. Although the pattern of setae on the tail is distinctly different from that of *O. sabulosus* in younger stadia, the presence of short but definite metazonite setae will confirm the animal as *T. niger*.

As in *O. sabulosus*, intercalary males are of common occurrence in this species. They may be recognized by a much smaller pair of first legs than in the immature male but not modified into the crochets of the mature condition; the gonopod gap is present but the gonopods within are not fully developed. There is a small ventral flange on the stipes, not so obvious as that of the functional male (Fig. 12).

Biology: Blower & Fairhurst (1968) and Fairhurst (1968, 1970, 1974) give details of the anamorphosis and life cycle in Britain. Eggs laid in spring reach stadia IV and V by their first winter and stadia VII and VIII (and IX?) by their second. Whilst maturity is achieved by stadium VIII (and very rarely by males at stadium VII), breeding does not normally begin until the third spring after birth at stadia VIII and IX, that is, by the slow developing females of stadium VIII and not by those which reached VIII at the end of their second year (Fairhurst, 1968). Usually the stadia of adult females most commonly represented in collections are VIII, IX and X in approximate proportion 1:2:1 with smaller numbers at stadia XI and XII. This suggests that breeding occurs first at three years old (stadia VIII and IX), secondly at four years, (stadia IX and X) and so on, a few females surviving two further years (at stadia X and XI, then stadia XI and XII) at five or six years old. By this argument, the occasional female of stadium XV may be up to nine years old.

Adult males are found mainly in stadium VIII, fewer at IX and fewer still at stadium X and beyond. Stadia VIII and IX will ideally moult after mating into intercalaries at stadia IX and X and then back into copulatory males at stadia X and XI by the next breeding season. Winter is usually passed in the intercalary stage but intercalaries may be found in the summer; intercalaries are known to moult, on occasion, directly into another intercalary stage. Fairhurst (1968, 1974) has shown intercalary males to be far less active than mature males; interpretation of pitfall trap data may be difficult. Then again, Blower & Fairhurst (1968), tentatively suggested that the spectrum of adult stadia found at any one site may be a function of the distance of the site from the optimum habitat, older animals having had more time for greater displacement.

Distribution

British Isles: First recorded and described by Leach (1815) and since this date has become one of the four most frequently encountered (and recognized) British millipedes (the others being *Cylindroiulus punctatus* (p. 152), *Ophyiolus pilosus* (p. 172) and *Polydesmus angustus* (p. 194). It is more frequent in base rich sites, especially in limestone districts and is thus the complement of the other British schizophylline *O. sabulosus* which prefers sandy places. *T. niger* appears to have fewer geographic limitations in the British Isles than *O. sabulosus*.

Tachypodoiulus niger, like its complement *O. sabulosus*, is a very vagile and eurytopic species. Its generic name means literally 'swift-footed-Julus'. It spends more time above ground than other millipedes, it can be found at night by torchlight high up tree trunks and walls; it sometimes rests by day within the canopy and can be beaten off on to a beating tray; it may rest in nooks and crannies of stone walls (it is sometimes seen ensnared within the meshed webs of *Amaurobius spp*). *T. niger* moves horizontally for considerable distances; it is sometimes forced to take shelter after a night of activity in all manner of places; it is most often noticed around and inside dwelling houses. The late Dr. Hugh Scott documented the visits of this species to his house at Henley-on-Thames. In 1958, for example, he recorded over 365 animals between 19 February and 28 April inside his house. It moves also into less hospitable places such as the sea shore where large numbers perish in the heat and dryness of the day. Fairhurst (1968, 1970, 1979) reports on the occurrence and behaviour of this species at Gibraltar Point, Lincolnshire coast and gives a fascinating account of the reactions and orientation mechanisms of the animals on the shore.

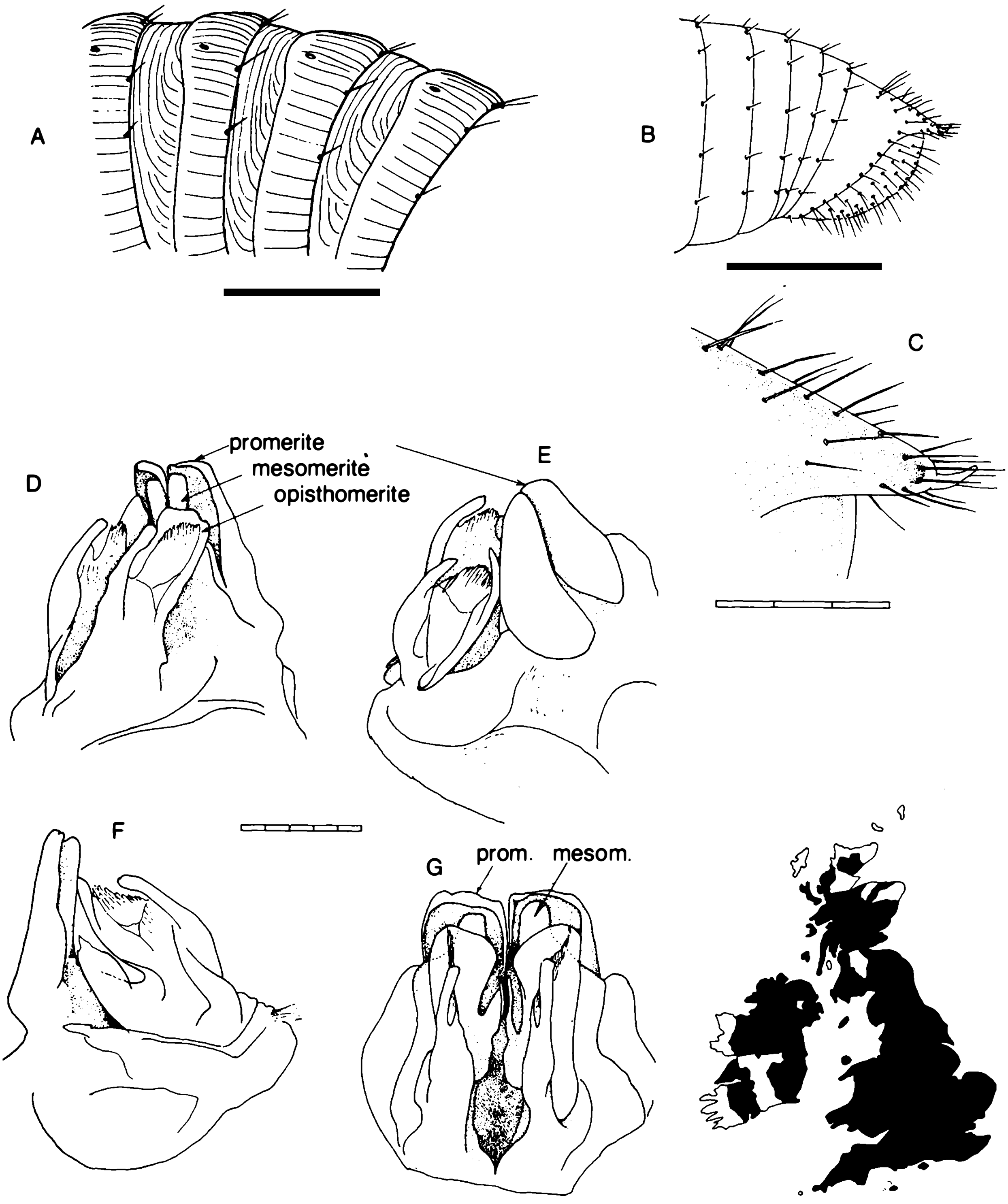


Fig. 42. *Tachypodoiulus niger*. A. Ventro-lateral view of mid-body rings to show ozopores posterior to the sutures and the transverse striae on the prozonites; B. Tail end showing upturned apex of caudal projection; note the presence of metazonite setae and the setae on the tail not confined to the apex (compare with Fig. 41B and C); C. Enlarged view of the upturned hyaline apex of the tail; D–G. Gonopods. D, Posterior lateral view; E, Antero-lateral view; F, Internal profile of left gonopod; G. Posterior view.

Whilst *T. niger* is one of the most frequently encountered of our snake millipedes, this is more a function of its vagility and its habit of resting under stones, logs etc., than of its abundance. In no place have I encountered densities of this species approaching those, for example, of *Ophyiulus pilosus* (p. 172).

Europe: Although *T. niger* is the commoner of our two schizophyllines it has the more restricted distribution on the continent; it is recorded mainly in the north and west: Holland, Belgium, France, Germany, Czechoslovakia, Switzerland and Austria but also from Spain. The biology and post-embryonic development of this species has recently been studied by Professor Sahli (see for example, Sahli, 1969b, 1978).

Tribe CYLINDROIULINI

Ten of the eighteen British julids belong to this tribe, nine are species of the single genus *Cylindroiulus*, the tenth is an *Enantiulus*. Cylindroiulini are indeed, closer to the perfect cylindrical shape than julids of the other tribes; they vary little in diameter along the trunk than the more fusiform (tapered at both ends) Julini and Schizophyllini; the Cylindroiulini are also stockier, shorter and fatter, than the Julini.

Without frontal setae on the head. Ozopores *on* the suture between pro- and metazonite. Usually without setae fringing the metazonites; the pre-anal ring is rarely extended as a pointed caudal projection; the telson and anal valves are rather sparsely setose. There are two exceptions to this latter suite of characters: *Cylindroiulus nitidus* (p. 150) and *Enantiulus armatus* (p. 164) possess metazonite setae, setose telson and pointed tail. Of the remaining eight species of *Cylindroiulus* we can note: *vulnerarius* (p. 147), without eyes, practically devoid of pigment and subterranean; *londinensis* (p. 140) and *caeruleocinctus* (p. 144), two related and quite distinctive species, and then a very homogeneous group of five species: *punctatus* (p. 152), *latestriatus* (p. 155), *britannicus* (p. 158), *truncorum* (p. 162) and *parisiorum* (p. 160) which were included in Verhoeff's sub-genus *Aneuloboiulus*. Of these five, *punctatus* is easily recognizable by its clubbed tail and closely-set metazonite striae; the other four are loosely referred to as the *luscus*-group since three of them were among the types of Meinert's *Julus luscus*. They are externally almost indistinguishable; all are 'latestriate' (except some individuals of *truncorum*), tailless and almost glabrous. *C. britannicus* and *latestriatus* can be separated from *C. truncorum* and *parisiorum* by the number of setae on the anal valves.

In all our species of *Cylindroiulus* except *C. nitidus* the cardines of the males are expanded. *Cylindroiulus* gonopods are characterized by a deep and clear division between anterior pro- and mesomerites and posterior opisthomerites, and by the possession of a flagellum and flagellum groove; these last are absent from the gonopods of *Enantiulus*.

Cylindroiulus londinensis (Leach)
(Fig. 43)

Julus londinensis Leach, 1815: *Trans. Linn. Soc. London*, *11* (2): 378
Cylindroiulus londinensis, forms *typica* and *finitimus* Ribaut, 1905, of Blower (1958) now *not* including *C. finitimus* (Ribaut, 1905)

Males and females 41 podous rings Length: 20–48 mm Diameter: 3.5–4.0 mm

Brown-black, almost black, greater in diameter than any other British julid. Caudal projection bluntly cylindrical, or quite distinctly clubbed or, occasionally, only very slightly produced. Trunk similar in diameter from head to tail like *C. caeruleocinctus* (p. 144), and unlike all other large brown-black julids in this respect. Metazonite striae more closely set than in *C. caeruleocinctus*, about one tenth of their length apart.

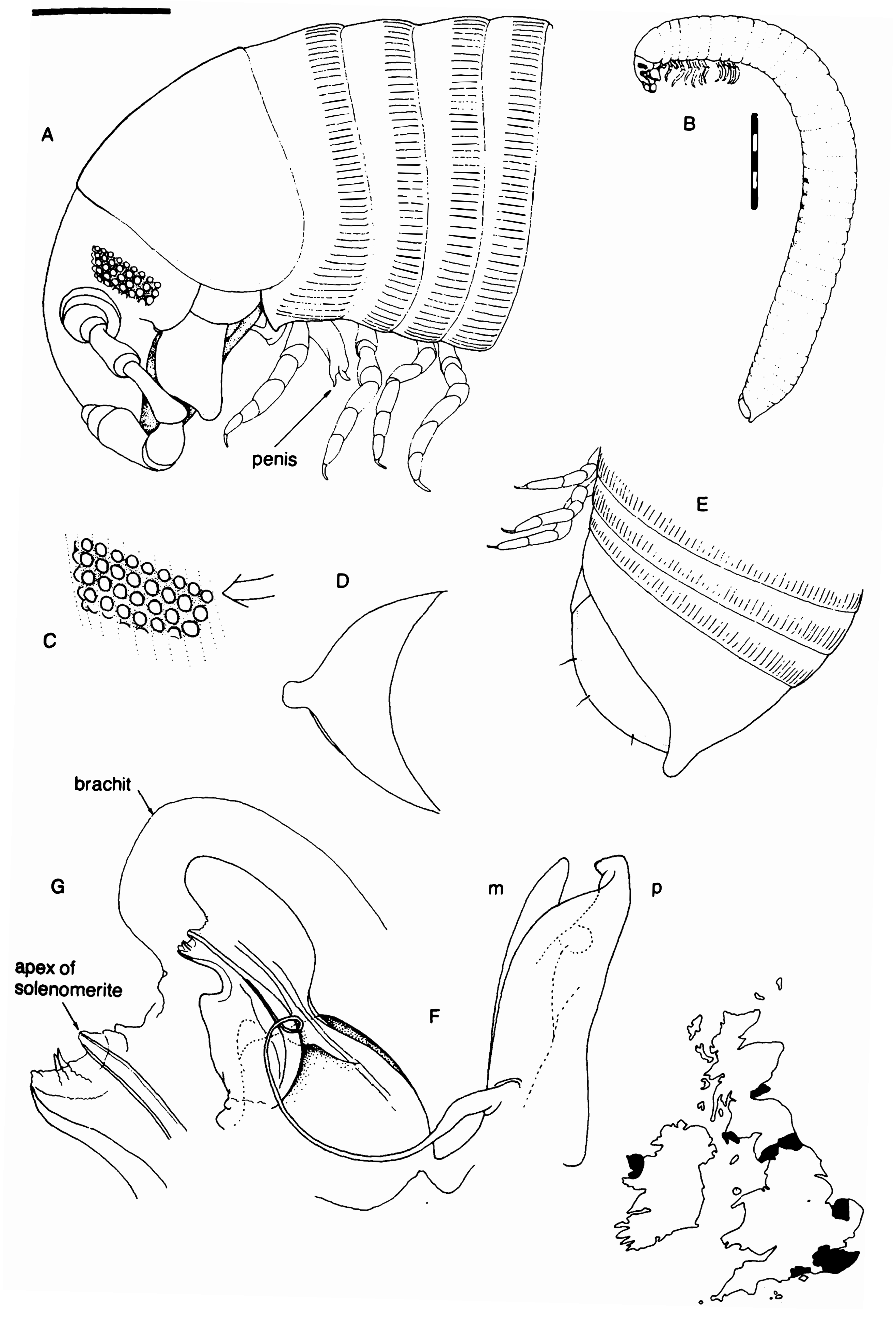
The gonopods are similar to those of *C. caeruleocinctus*; comparison of Figs. 43 and 44 clarifies the subtle differences: the brachit of *londinensis* is more expansive than that of *caeruleocinctus*; its outer (anterior) edge runs roughly parallel to the solenomerite; in *caeruleocinctus*, the edge of the brachit converges on to and beyond the solenomerite apex. The brachit extends beyond the apex of the solenomerite slightly further in *londinensis* than in *caeruleocinctus*, but this character is not so usefully discriminating as Mauriès (1964) shows for *londinensis* and *finitimus*.

The opisthomerite of *C. londinensis* does not have the deep cleft between the apex of the solenomerite and the brachit which is evident in *C. caeruleocinctus* (compare Figs. 43 and 44). Immediately posterior to the apex of the solenomerite are two flat pointed processes; in *caeruleocinctus* there are five or six, but I have examined too few individuals of *londinensis* to be certain that this is a useful discriminant feature.

Historical note

In Blower (1958) I followed Brade-Birks (1922, 1939) in regarding Leach's type of *londinensis* and the variety *finitimus* of Ribaut as larger, older, individuals of the more common variety *caeruleocinctus* of Wood, well-known

Fig. 43. *Cylindroiulus londinensis*. A. Head end of a stadium XI male; note the extended bilobed penis behind the second pair of legs; it is not visible in the same view of *C. caeruleocinctus* (Fig. 44), but this is merely a circumstance of post mortem contraction and is not a specific characteristic; B. Outline drawing of the same male as A; C. Enlarged view of the ocular field in the same position as in A. Note that the four or five rows of ocelli immediately apparent are *not* the incremental additions; to see these observe from the position of the arrow. The 'antennal limitation' to the field in this species (and in *C. caeruleocinctus*) is more marked than in other species (compare with Figs. 12 and 53); D, E. Tail end, D, in dorsal view; E, in lateral view, showing clubbed apex; F. Internal profile of left gonopod (the looped flagellum is an artefact of dissection); G. Enlarged view of the apex of the opisthomerite; note the solenomerite apex flanked by two teeth.


A
penis
B
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apex of
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on the continent as *C. teutonicus* (Pocock). Although the difference in the frequency of the metazonite striae between *londinensis* and *finitimus* on the one hand, and *caeruleocinctus* on the other, is striking, a similar difference is seen between males and females of *C. truncorum* (p. 162), and even along the length of the same male.

The most extensive British material available to me was collected by Mr. Kime from Ryhope Dene in Durham in 1968. I am grateful to him for letting me have the notes of his examination and the material itself from which I have prepared the drawings of the gonopods. Kime noted that his animals were 20–40 mm long and that even average sized individuals (*circa* 28 mm) had the prominent clubbed caudal projection, and one of the larger females had a short caudal projection indicating that the form of the tail does not appear to be a function of size.

Mauriès (1964) agreed with Ribaut (1905) that *finitimus* was closely similar to *londinensis* in external appearance (similar size and strial frequency), but discovered a distinct difference between the gonopods of these two forms; the gonopods of *finitimus* were very similar to those of *caeruleocinctus* and quote distinct from those of *londinensis*. Mauriès also recalled that Brolemann (1927) had shown that the vulvae of *finitimus* and *caeruleocinctus* were, in some respects, more similar to each other than to those of *londinensis*.

Mauriès (1964) illustrates a range of caudal projections in *londinensis* from almost absent to a simple cylindrical process, through to a distinctly clubbed projection; he also figures some variation in the tails of *finitimus* (as defined by *caeruleocinctus*-type gonopods and *londinensis*-type striae), but the tail of *finitimus* is never cylindrical or clubbed. *C. finitimus*, according to Mauriès, an upland species restricted to a small area of the west and central Pyrénées. Thus the large animals reported in Britain with less well-developed tails come within the range of variation of *C. londinensis* and have been referred to the form *finitimus* in error.

Distribution

British Isles: First recorded and described from 'near London' (VC21?) by Leach (1815). Jackson (1915) recorded the rediscovery of the species in Eggerslack woods, near Grange in Lancashire (VC69) by Mr. Standen in 1914 and again in 1915 together with *C. caeruleocinctus*. Brade-Birks (1918c) recorded both sexes of *londinensis* and also a female he referred to the var. *finitimus* from near Dartford in West Kent (VC16); later, Brade-Birks (1920c) recorded *londinensis* var. *finitimus* from near Castle Rising in Norfolk (VC28).

Mr. John Sankey collected four females of the typical *londinensis* from Westwell, near Ashford in East Kent (VC15); the two largest each had 41 podous segments and measured 30 × 3.75 mm and 33.5 × 4.00 mm (the tail end of the latter appears in Fig. 40A). Mr. Sankey also sent to me a female from Box Hill in Surrey collected in June 1956 which was 3.5 mm in diameter and had a tail similar to that described by Ribaut for his *finitimus*. I have already mentioned the extensive collection of this species from Ryhope Dene in Durham (VC66) by Mr. Kime; he found the animals in an ash wood with blackthorn and elder scrub, in April 1968. Jackson (1982) reports that the species is still to be found in Ryhope Dene, but that it has not been recorded from Castle Eden Dene or Hawthorn Dene.

Kime (1978) commented there was only one Km square in which he had found both *C. londinensis* and *C. caeruleocinctus* together. This was a wood near Orpington in Kent; in his experience, the two species are usually found in separate places. The most recent records from the millipede survey are from Hampshire (VC11), Wigtown in Scotland (VC74) and West Mayo (VCH27) in the Irish Republic.

Europe: Mauriès (1964) gives a map of the distribution of *C. londinensis*, *C. caeruleocinctus* and *C. finitimus*; both the former are shown to occupy most of France; *londinensis* is shown tentatively extending into north western Spain and Portugal. Demange (1981) lists *londinensis* as widely distributed throughout France, in woodland and open land up to 2,100 metres.

Cylindroiulus caeruleocinctus (Wood)
(Fig. 44)

Iulus caeruleocinctus Wood, 1864: *Proc. Acad. Nat. Sci. Philad. 1864*: 10–16
Julus teutonicus Pocock, 1900: *Ann. Mag. nat. Hist.* (7) *6*: 206–207
Cylindroiulus londinensis var. *caeruleocinctus* (Wood) of Brade-Birks (1922) and in Blower (1958)

Sexual dimorphism at stadium VIII

Males	IX–XIII	32–34	Length: 20.2–25.7 mm	Diameter: 1.80–1.92 mm
Females	IX–XIV	32–46	22.7–29.2	2.04–2.64

Measurements of animals collected in the Cotswolds in summer are for stadia XI to XIII (males) or XIV (females). Schubart's figures are similar except that his range of lengths exceeds ours, especially at the upper end (males up to 32 mm, females up to 37 mm).

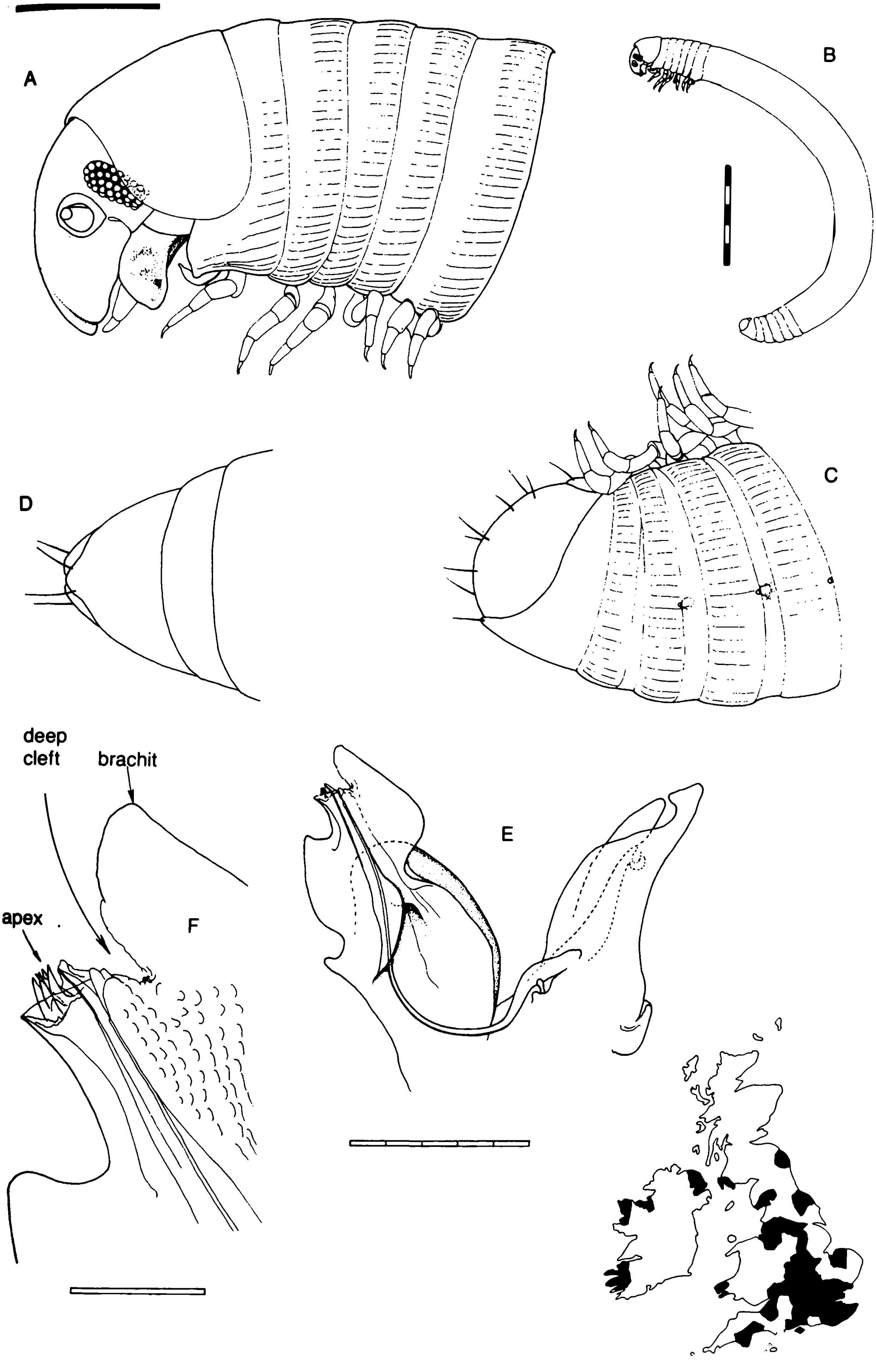
This is the only tailless julid in Britain which is brown-black: all other darkly coloured julids (*Julus scandinavius, Ophyiulus pilosus* and *Tachypodoiulus niger*) have distinct pointed tails, except occasional older individuals of *Cylindroiulus truncorum* and *C. latestriatus* which are much smaller. It is quite distinctive amongst our large black julids in having a more or less constant diameter from head to tail and in having a metallic 'sheen' caused partly by air included in the inter-ring joints. It is similar in these respects to *C. londinensis* and indeed was considered as a variety of *C. londinensis* in the first edition; see the historical note in the description of this last species.

Biology. Data on the course of anamorphosis (see Fig. 9) were surmised from limited British material (limited in representation of younger stadia) chiefly from Reading, Berkshire and Woodchester Park in the Cotswolds, and the resulting scheme agreed in all important respects with that of Sahli (1969b); data (in Fig. 9) for stadia II–IV are given from Sahli. Immature males are present in all stadia from VIII–XII which allows for males from stadium IX–XIII.

Distribution

British Isles: First recorded by Pocock (1900) from near Sevenoaks in Kent and now with a recorded distribution chiefly in the south and east of England following, rather imperfectly, the distribution of Jurassic limestone and chalk. While recorded in the north west and south west, it is by no means common there. Kime (1978) ranks the species seventh in his survey area of Surrey,

Fig. 44. *Cylindroiulus caeruleocinctus.* A. The head and rings I–VI of a stadium XI male; B. Outline drawing of the whole animal partly seen in A; C. Terminal rings of the same animal as in A and B; D. Tail end in dorsal view; E. Internal profile of the right gonopods; F. Enlarged view of the apex of the opisthomerite showing the apex of the solenomerite fringed with five teeth. Note in A that the collum overlaps the ocular field and makes it difficult to interpret; it is easily moved away with a mounted needle.


A
B
C
D
deep cleft
brachit
apex
F
E

Sussex and Hampshire, compared with the thirteenth in England in Blower (1972), but notes that it is absent from west Sussex and in the clay belts. In Surrey, Kime ranks the species sixth. In 1980 the species is ranked twentieth in England; like *Blaniulus guttulatus*, it appears to have been less frequently recorded during the 1970's.

C. caeruleocinctus is usually found in calcareous soils under cultivation. Morris (1922, 1927) found it in his survey of the soil fauna of the famous Broadwalk fields at Rothamsted. There are many records of this species attacking crops, especially potatoes, here and in Europe (see, for example, Brade-Birks (1930)). Davis (1982) found the species commonest in pitfall traps in London gardens, rarely in soil and litter samples; he found a large colony in stacked, sawn tree stumps. Curiously, my only meeting with the species in the west, in number, was in a stack of newly sawn logs at Woodchester Park, near Nailsworth in Gloucestershire.

Europe: Mainly northern and central: Norway, Sweden, Esthonia, Lithuania, Holland, Belgium, Denmark, France, Germany, Poland, Czechoslovakia, USSR (European plain), Switzerland and, furthest south, Yugoslavia.

Introduced into the USA and Canada. Abundant throughout the New England States and adjoining parts of Canada, southwards to Pennsylvania and Maryland, westwards to Indiana, Illinois and Iowa (Chamberlin & Hoffman, 1958).

Cylindroiulus vulnerarius (Berlese)
(Fig. 45)

Mesoiulus vulnerarius Berlese, 1888: *Acari Miriapodi e Scorpioni italiana* fasc. *48*, No. 1, pl. 1, Figs. 1–7

Male	VII & VIII(?)	37–42	Length: 12.4–15.3 mm	Diameter: 0.99–1.13 mm
Female	VII–XI(?)	38–50	12.8–21.8	1.12–1.58

Measurements of two from London, three from Manchester and ten from Glamorgan (6♂♂, 9♀♀).

Mostly without pigment but with amber colour of heavier sclerotization on the extremities: the ventral edge of the head capsule, the tip of the gnathochilarium, the apex of the caudal projection and the edges of the anal valves. The animal has no epidermal pigment; most of the animal is basically cream due to the light amber colour of the sclerotized outermost layer of the cuticle. The ozadenes are orange rather like those of *Archiboreoiulus pallidus* (p. 118). The trunk of older adult individuals takes on an overall greenish hue like that of *C. nitidus* (p. 150) due to the dark contents of the gut showing through the amber tint of the cuticle. Younger animals present overall a cream orange appearance.

This is the only julid in Britain without ocelli and with a caudal projection. The tail recalls that of *C. nitidus* in being slightly ventrally directed but is much more blunt. There are a pair of setae on the caudal projection, another pair on each anal valve and a pair on the anal scale, otherwise the trunk is quite glabrous.

Distribution

British Isles: This blind julid is one of the most recent additions to the British fauna. Dr. Adrian Rundle found a male of this species under a brick in the back yard of the 1st Mortlake scout headquarters in April 1976 and a fortnight later found a female in soil beneath deciduous litter near the refreshment pavilion in the Royal Botanic Gardens, Kew; after the identity of these was established, he found further examples collected in 1975 from a garden in Kew and from a site near Barnes railway station.

In April and May 1978 Mr. Martin Jones had a male and two females in pitfall traps he had set at Fletcher Moss, Didsbury, Manchester. In November 1978 Mr. Declan Doogue found the species in soil by a derelict building at Glasnevin, Dublin.

In September 1979 a party of students and I were collecting in the azelea bed of Singleton Park, Swansea, immediately adjacent to the campus of the University College and came across animals similar in appearance to *Archiboreoiulus pallidus* which were clearly julids and Michael Meharg turned up a large olive green female which proved to be an adult *C. vulnerarius.* We paid further visits to the site and collected 11 adults and 20 immature individuals (mainly stadia III and IV).

Thus within four years of the first British record an abundance of material from two English counties, one Welsh and one in the Irish Republic has been collected. Most recently Dr. Davis has had the species from the Chelsea Physic garden and Holland Park, London (1982).

Europe: According to Schubart (1934) this species is native to north central Italy, Florence and the estuary of the Frigido. He refers to Lohmander's record of this species from a greenhouse in Gothenburg. Since Schubart's monograph the only other records I can find are from Holland and Belgium.

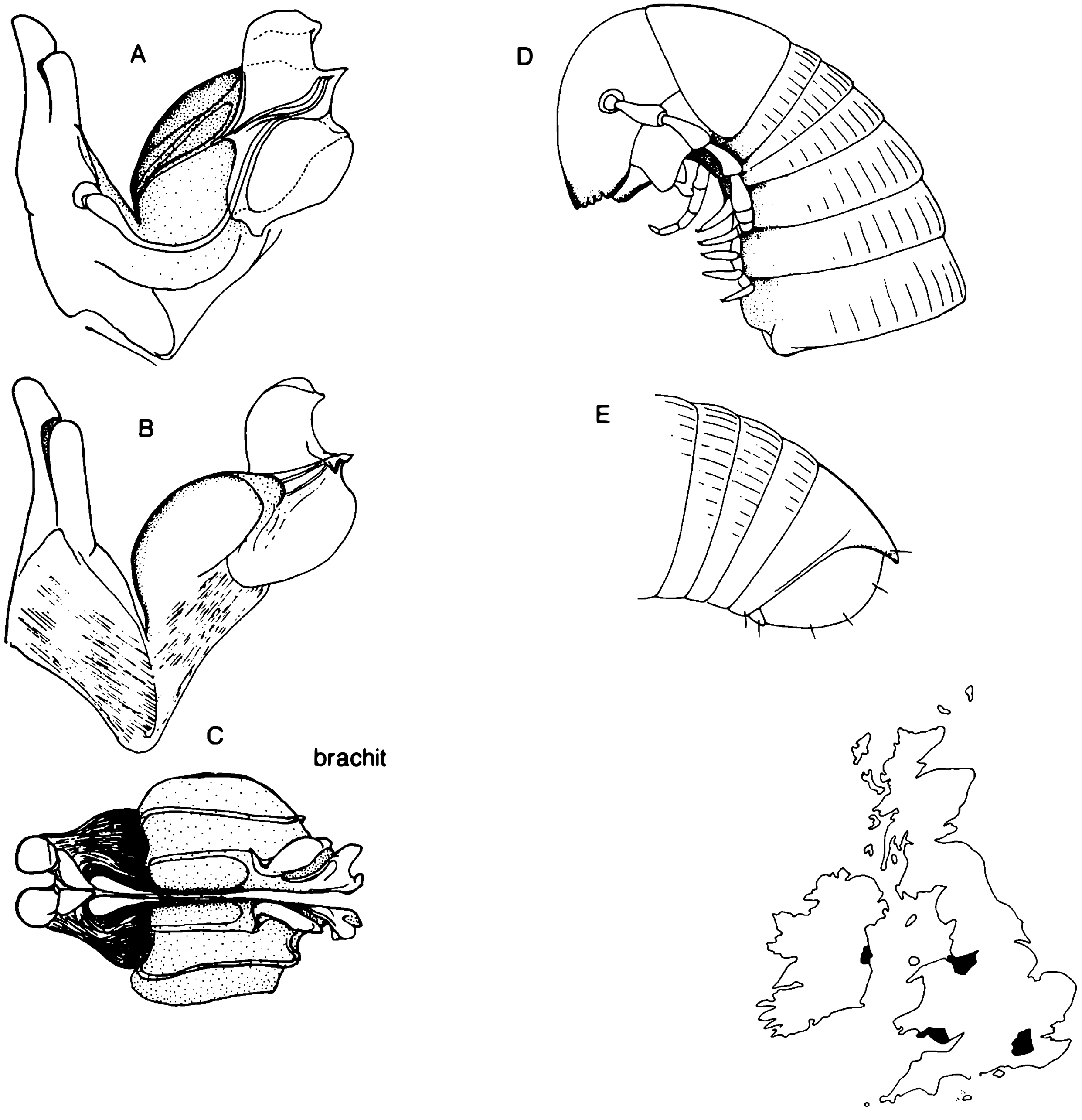


Fig. 45. *Cylindroiulus vulnerarius.* A–C. Gonopods. A. Internal profile; B. External profile; C. Ventral view of both pairs; D. Head and rings I to VII of male; to show complete absence of ocelli and amber colouration at tip of labrum and gnathochilarium; E. Tail end; only the very apex of the caudal projection and edges of the anal valves are amber coloured.

Cylindroiulus nitidus (Verhoeff)

(Fig. 46)

Julus nitidus Verhoeff, 1891: *Berliner Entom. Ztschr.*, *36*: 148–150, pl. 8, Figs. 43–45

Sexual dimorphism at stadium VI

Male	VIII–XIII	37–54	Length: 11.0–21.6 mm	Diameter: 0.94–1.42 mm
Female	IX–XII	(41)42–52	13.5–24.8	1.13–1.81

Dimensions from a population at Mill Dale in Derbyshire. Schubart's (1934) range extends to 60 podous and includes males up to 29 × 2.0 mm and females up to 32 × 2.4 mm.

The lightest coloured of our julids (except the blind *C. vulnerarius* (p. 147) and *Metaiulus pratensis* (p. 180)). Tan to light brown with darker brown ozadenes sometimes with a reddish tinge. The gut contents show through the amber coloured cuticle to give a greenish tinge. *C. nitidus* is the only British member of the genus with a pointed tail (the tail in *C. vulnerarius* is much more blunt); the caudal projection is superficially similar to that of the julines but is readily distinguished in being slightly ventrally directed. As in other species of *Cylindroiulus* the ozopore lies *on* the suture between pro- and metazonite, not posterior to the suture as in the julines, and there are no frontal setae.

Biology. Blower & Miller (1977) have described anamorphosis and life history in a woodland population in the limestone district of Derbyshire. The pattern of ocelli in this species is not easily interpreted; the individual rows added at each moult are by no means clear. The succession of stadia was followed by probability analysis of lengths and diameters. The species is iteroparous, females surviving their first breeding season to breed again in a later season, but it is unique among the Julidae in having a succession of mature male stadia as well as females. Verhoeff found a few intercalary males but Sahli (1969a) demonstrated that mature males could moult directly into a further mature stadium, retaining the fully developed gonopods, without the interpolation of an intercalary stage. In the Derbyshire population males occur in stadia VIII to XIII and not one intercalary has been observed. Sahli (1982) has recently examined material from Mill Dale in Derbyshire and has found one male which has the first pair of legs of the *rhenanus* type; this is a condition intermediate between the intercalary and adult (see Sahli, 1969a).

Eggs laid in spring and summer develop to stadia III or IV by their first winter; animals are mainly at stadium VI for their second winter and stadia VII and VIII by their third. Males may therefore become mature in three years but females do not mature until stadium IX and therefore take four years. Assuming mature animals moult just once a year as Sahli (1973) found, both males and females survive a further three to five years to an age of seven, eight or nine years.

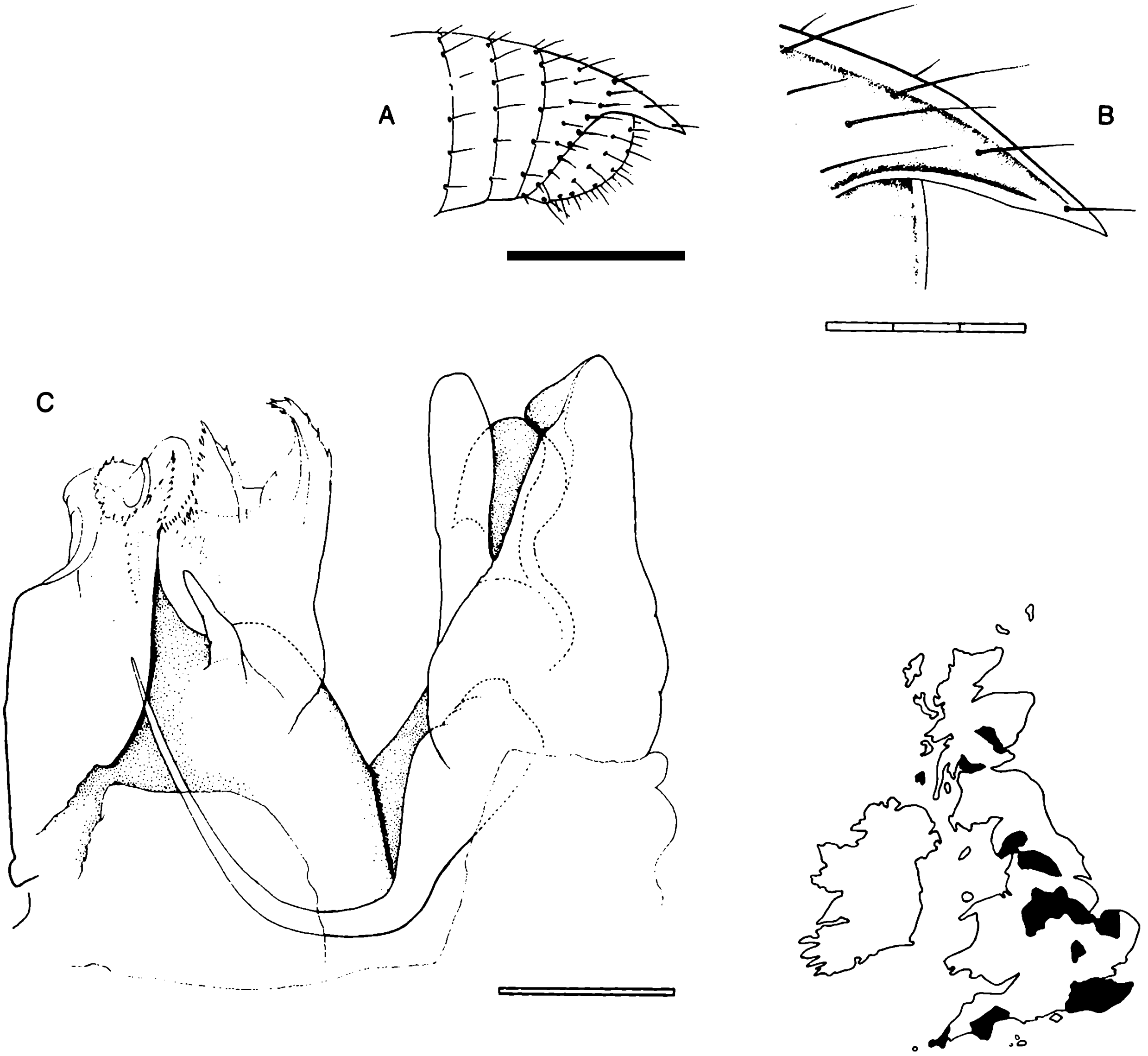


Fig. 46. *Cylindroiulus nitidus.* A. Tail end showing slightly downturned caudal projection; B. Enlarged view of caudal projection; C. Internal profile of right gonopods.

Distribution

British Isles: First recorded by Brade-Birks (1917a) from under a stone on the roadside grass verge by Winkhill, north Staffordshire. The first edition included three more vice-county records from Lincolnshire south (VC53), Norfolk west (VC28) and Cornwall (VC1), and in Blower (1972) twelve vice-counties are listed. Since 1970 only seven more records have been added and so it is still to be regarded as a rare animal. However, in the areas of its occurrence it can be abundant; Blower & Miller (1977) record densities of 50–180 per square metre over a period of ten years at Mill Dale in Derbyshire.

C. nitidus is the palest of our eyed snake millipedes and is also the most subterranean, which may account for the paucity of records. In my experience it is associated with limestone soils but Kime (1978) found it on sandstone.

Europe: Norway, Sweden, Denmark, Holland, Belgium, France, Germany, Switzerland, Poland, Czechoslovakia and west Tyrol.

Cylindroiulus punctatus (Leach)
(Fig. 47)

Julus punctatus Leach, 1815: *Trans. Linn. Soc. London*, *11* (2) 379
Cylindroiulus silvarum (Meinert) of continental authors

First sexual dimorphism at stadium VI

Male	VIII–IX (X)	41–47	Length: 14.2–17.5 mm	Diameter: 1.17–1.31 mm
Female	VIII–XIV	40–54	14.0–27.0	1.35–2.00

Dimensions of animals from a Devon oak wood

Straw to light brown, sometimes a little darker, ozadenes much darker brown. Metazonite striae deep and closely set compared with the 'latestriate' condition of the '*luscus*' group, *C. latestriatus, britannicus* etc. This character of the clearer, more numerous striae enables younger stadia of *C. punctatus* with poorly developed caudal projections to be separated from the tail-less species of the *luscus* group. In adults and later immature stadia, the caudal process of *C. punctatus* is quite distinctive. As in the *luscus* group of species, there are no setae fringing the metazonites.

Biology. The anamorphosis or progression of stadia in this species was described by Saudray (1952). It is in this paper that Saudray first demonstrated that in a julid a new row of ocelli is added to the ocular field at each moult. Sahli (1955) followed the progression of stadia in the Saar and the Ardennes and reported a few differences between his animals and those from Normandy described by Saudray; Saudray found the first mature stadium was IX whereas Sahli found most of his animals were mature by stadium VIII. Blower & Gabbutt (1964) studied a population in a Devon oak wood; they separated stadia by probability analysis of lengths and diameters since they had found difficulty in interpreting the ocular field in the species associated with *C. punctatus*, *C. latestriatus*. The progression in Devon was found to be similar to that described by Sahli in French material in that maturity is first achieved at stadium VIII and that a total of thirteen or fourteen stadia are recorded. Sahli's animals had higher increments in stadia VIII and IX (i.e. higher numbers of apodous segments) and correspondingly higher numbers of podous segments, three to six in females and up to ten in males. Sahli records differences in increment even between different areas of France and it will be useful to document stadia and segment numbers found in different areas of Britain.

In the Devon population, newly born animals appear to reach stadia (III), IV and V by their first winter and up to stadium VII by their second. Since maturity is not achieved until stadium VIII or IX, three years must elapse between generations. Females having oviposited at stadium VIII or IX must survive and breed in several subsequent years to reach stadium XII and occasionally beyond. Males do not moult again after first achieving maturity in either stadium VIII or IX. As in France, in other parts of Britain

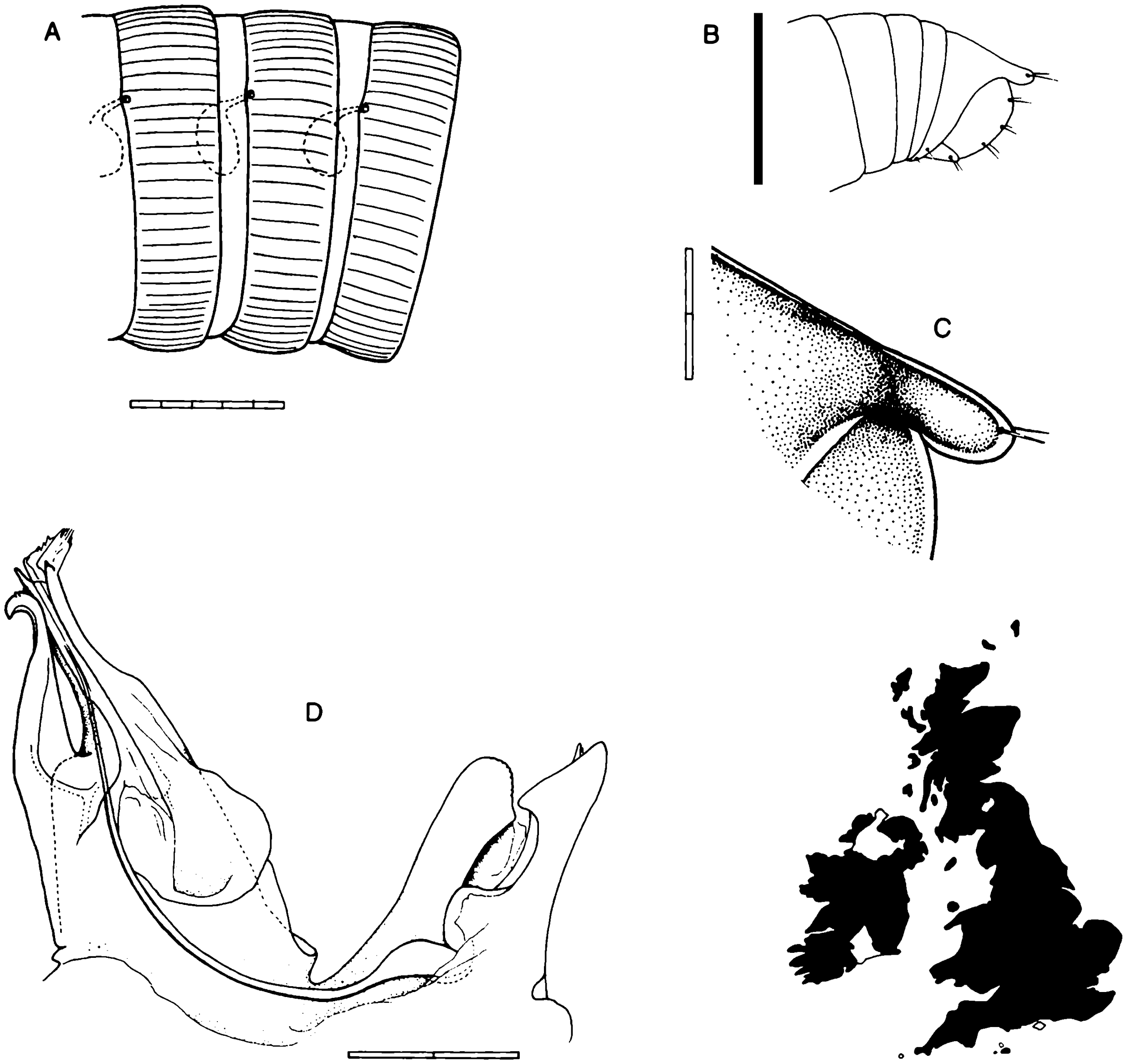


Fig. 47. *Cylindroiulus punctatus*. A. Three mid-body rings to show the closely set striae (compare with the 'latestriate' condition in Fig. 48); B. Tail end showing clubbed caudal projection; C. Enlarged view of apex of caudal projection; D. Internal profile of the right gonopods.

males may reach stadium X (i.e. by passing through stadia VIII and IX as immatures).

Distribution

British Isles: First recorded in Britain and described by Leach (1815), it was soon established as the most frequently recorded millipede on the British list. The Scottish vice-county without a record must surely be found to be occupied before long. Similarly, there seems no good biological reason why any parts of Ireland should be unoccupied.

One of the reasons for the frequency with which this species is encountered is its habit of living under the bark and in dead wood and extending its range into quite acid situations. In addition to being the commonest millipede associated with dead wood it is also found in slowly decomposing deciduous leaf litter of the less palatable species of deciduous trees and in the humus beneath; in these situations, in acid woodland on sandy soil for example, it is sometimes a common animal as in the Devon oak wood referred to above and in beech woods with a thick layer of litter. It extends into sandy heathland soils but is rarely present in arable or grassland.

Europe: Confined to the north and west of the continent: Norway, Sweden, Finland, Denmark, Holland, Belgium, France, Germany and northwest Poland; but also found in Barcelona, Spain.

Outside Europe has been reported from Newfoundland.

Cylindroiulus latestriatus (Curtis)
(Figs. 12, 48)

Julus latestriatus Curtis, 1845: *Jour. Roy. Agric. Soc. Eng.*, 5(1) 229 in part
Cylindroiulus latestriatus (Curtis) Brade-Birks, 1928: *Ann. Mag. nat. Hist.* (10) *1*, 397–398 (lectotype)
Cylindroiulus frisius (Verhoeff) of continental authors
Cylindroiulus owenii (Bollman) of previous British authors (see Blower, 1953)

Sexual dimorphism at stadium V

Male	VII–IX	30–37 (39)	Length: 8.6–12.5 mm	Diameter: 0.81–1.03 mm
Female	VII–XIII	30–43	8.7–16.0	0.94–1.37

Females with 40+ podous almost black

Light brown with darker ozadenes but not especially conspicuous; sometimes the body is darker and older individuals can be almost black like *Ophyiulus pilosus* (p. 172). Metazonite striae widely spaced as the trivial name suggests. Anal valves usually with three setae each. These last two characters are also possessed by *Cylindriolus britannicus* (p. 158) which can only be distinguished by subtle differences in colouration, (especially the rich red ozadenes of *britannicus*.)

Biology. Details of anamorphosis and life cycle for a population in a Devon oak wood are given by Blower & Gabbutt (1964). The pattern of ocelli in this species is rather difficult to interpret and the stadia were separated by probability paper analyses of lengths and diameters. Cotton & Miller (1974) worked on a duneland population on the east coast of Scotland; they suceeded in separating stadia by means of the ocelli and their stadia agreed in the main with those suggested by Blower & Gabbutt.

The animal is iteroparous like *C. punctatus* (p. 152), females surviving first reproduction to breed again in further seasons, but not the males. Animals progress to stadia (III), IV and V by their first winter and reach stadia VII and VIII by the second, but unlike the condition in *C. punctatus*, maturity is achieved by stadium VII and breeding therefore occurs in the second spring after birth. Females continue to moult and survive for a further three or more years after first becoming mature. This much refers to the Devon population. Deshmukh (1974), working in the same dune area of Scotland as Cotton & Miller found that his animals took three years to reach maturity.

Distribution

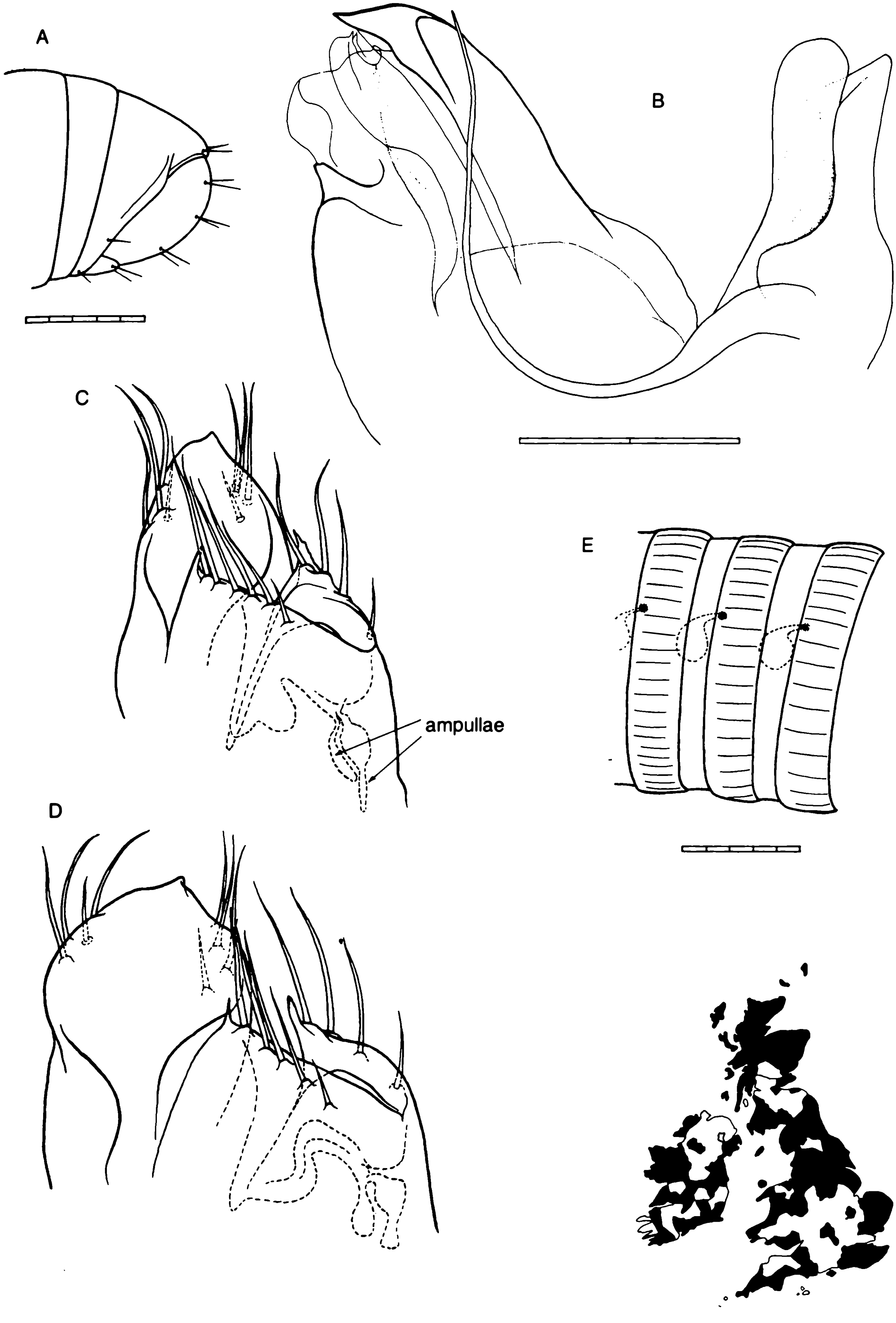
British Isles: First recorded and described from Nantwich in Cheshire (associated with *C. parisiorum*) 'attacking crops' by Curtis (1845). Since this time the species has been found repeatedly in coastal districts and was recorded until 1953 under the name of *C. oweni*. It has now been recognized in most counties with a coastline; it has occasionally been found inland but rarely from inland counties, e.g. Surrey, Salop, Montgomery, Suffolk west, Nottingham, Oxford, Huntingdonshire, Derbyshire and Yorkshire, but for the most part it is confined to the coast or a few miles from it. More frequently found inland in Ireland; it is the fifteenth most commonly recorded species in Blower (1972) and has since been elevated to the twelfth (Fairhurst, Barber & Armitage (1978)), where it remains (1980); it is thus more frequently recorded than *C. britannicus* (p. 158) which has no such geographical limitation.

It occurs on fixed and semi-fixed dunes at the roots of marram grass, on the shore in the roots of sea pink and other halophytes, most often in very sandy soil but also in deciduous leaf litter (as at Harpford wood in Devon).

Europe: Confined to north west Europe and there mainly found in gardens, greenhouses and other situations associated with human activity. Norway, Sweden and Finland; Holland, Belgium, France, Germany, Switzerland, Poland and Czechoslovakia. Also from Spain and Portugal.

Introduced into Canada, USA and as far afield as Peru, Mas-a-tierra (Chile), St. Paul Island (Antarctica), Gough Island in the Atlantic and Mexico.

Fig. 48. *Cylindroiulus latestriatus.* A. Tail end showing anal valves with three pairs of setae; B. Internal profile of right gonopods (compare with *C. britannicus*, Fig. 49B and see also Fig. 13); C. Posterior view of left vulva; D. Posterolateral view of left vulva; note the more-or-less symmetrical operculum and the single row of setae on each side of the bursa (compare with Fig. 49C and D); E. Mid-body rings to show widely spaced ('latestriate') condition of striae and the ozopore in contact with the suture.


A
B
C
ampullae
E
D

Cylindroiulus britannicus (Verhoeff)
(Fig. 49)

Julus britannicus Verhoeff, 1891: *Berliner Entom. Ztschr.*, *36*: 147–148, pl. 8, Figs. 41 and 42

Sexual dimorphism at stadium V

Male	VII–IX	32–40	Length: 9.5–10.8 mm	Diameter: 0.85–0.90 mm
Female	(VII) VIII–X	32–43	10.6–15.9	1.12–1.50

Light to medium brown but with much brighter coloured ozadenes than *C. latestriatus* (p. 155); these are rich red, almost the colour of those of *Blaniulus guttulatus* (p. 116) and *Ophyiulus pilosus* (p. 172); the ozadenes give the living animal a purplish appearance, especially the younger stadia which resemble those of *Ophyiulus pilosus* in colour. The metazonite striae are widely spaced and the anal valves have three pairs of setae like *C. latestriatus*.

The majority of the males mature at stadium VII and most of the females in stadia VIII–X. There is not the same evidence for survival after the first breeding season in this species as with *C. latestriatus*; animals at stadia VIII, IX and X may all achieve maturity at the same time representing slow, average and rapid development.

Distribution

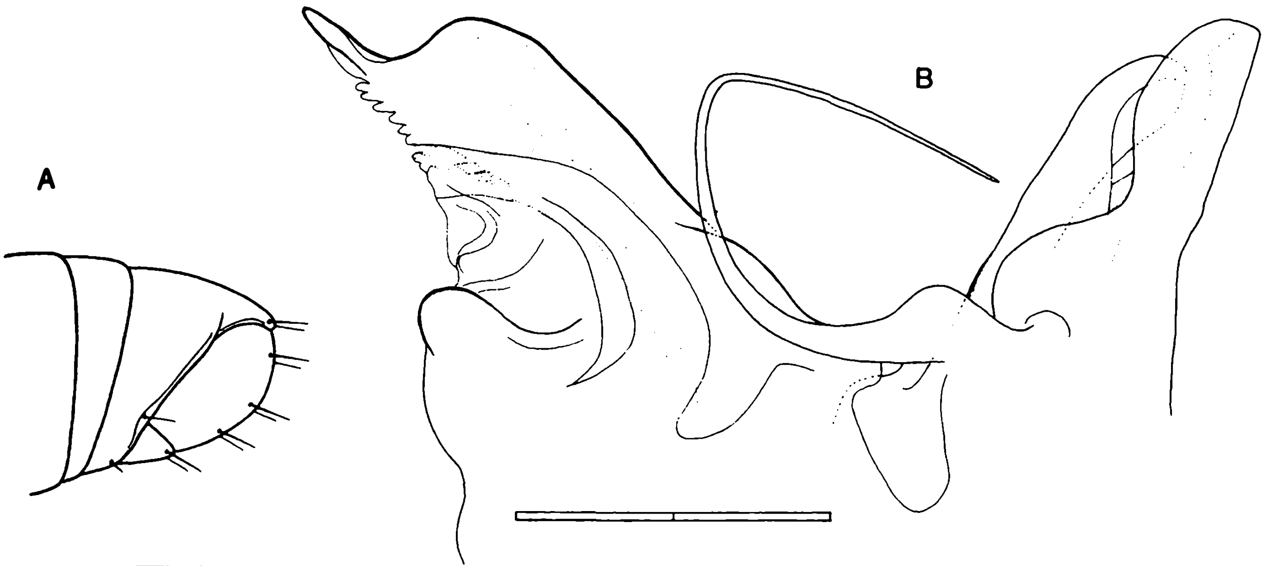
British Isles: First recorded by Evans (1907) from Scotland and since found from many English vice-counties but not so frequently in Scotland, Wales and Ireland. The distribution is understandably not so well known because of the difficulty of separating the species from its close relatives, but it has moved from eighteenth position in 1973 to fifteenth in 1980 in the British Myriapod Survey.

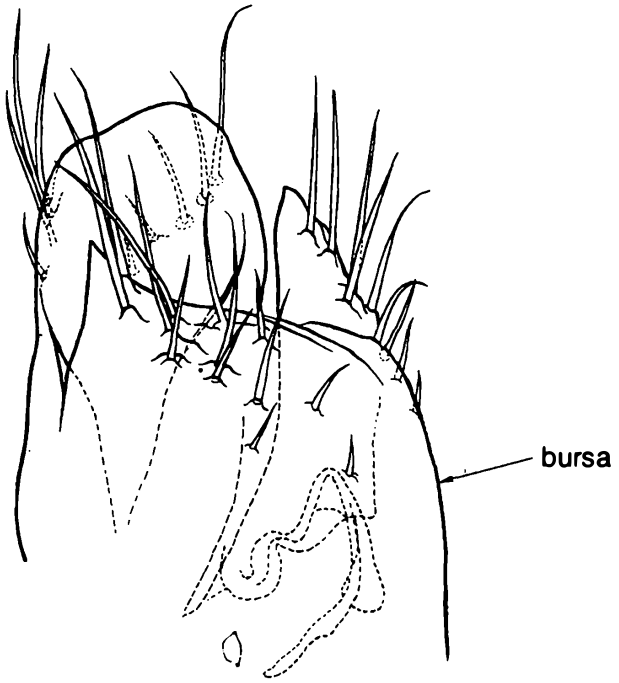
It is most often found beneath the bark of dead deciduous tree trunks and stumps and in the wood beneath and is often associated with *C. punctatus, Proteroiulus fuscus* (p. 107) and *Nemasoma varicorne* (p. 102). This habitat is never (hardly ever) occupied by *C. latestriatus. C. britannicus* is sometimes found in the soil, but usually close to dead wood or slowly decomposing leaf litter.

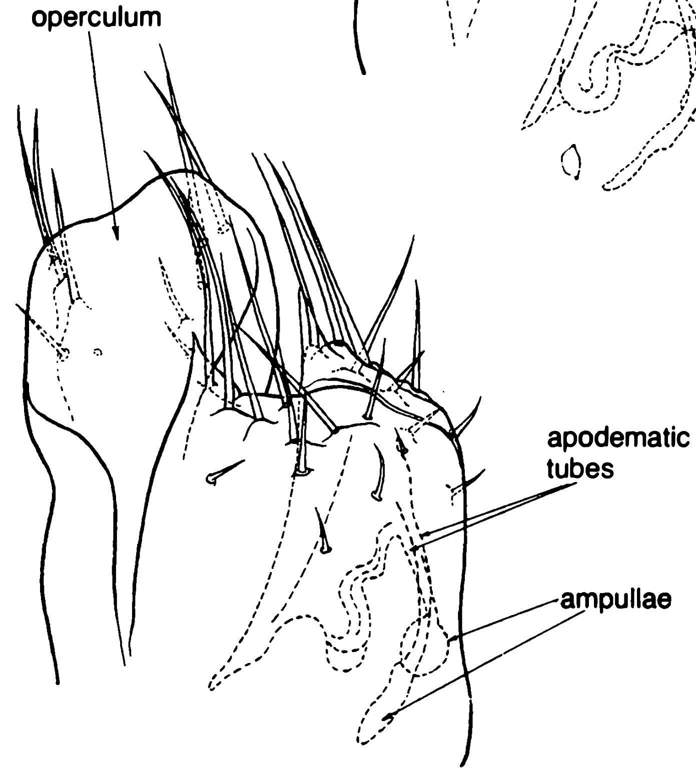
Europe: Slightly more restricted in Europe than *C. latestriatus* but again with a predominantly north west distribution: Norway, Sweden and Finland; Holland, Belgium, Denmark, Germany and Poland. Mainly synanthropic.

Like *latestriatus*, widespread outside Europe. Schubart gives St. Miguel (Azores), Madeira, Portugal and South Africa. Also USA, Newfoundland and New Zealand.

Fig. 49. *Cylindroiulus britannicus.* A. Tail end to show absence of caudal projection and three pairs of setae on the anal valves; B. Internal profile of right gonopods. Note the finger-like projection, sometimes reflexed more in the direction of the arrow (compare with Fig. 48B); C. Posterior view of the left vulva; D. Posterolateral view of left vulva; note the more asymmetric operculum and the more extensively and haphazardly setose bursa (compare with Fig. 48C and D).


A
B


C
bursa


D
operculum
apodematic tubes
ampullae

Cylindroiulus parisiorum (Brolemann & Verhoeff)
(Fig. 50)

Julus parisiorum Brolemann & Verhoeff, 1896: *Feuilles Jeunes Naturalistes* (3) *26*: 214–217, Figs. 1–4 and 7

Cylindroiulus ignoratus Attems, 1926

Sexual dimorphism at stadium V

Male	VII–IX	30–37	Length: 9.2–9.8 mm	Diameter: 0.73 mm
Female	VII–X	30–39	(9.0)9.6–12.2	0.92–1.10

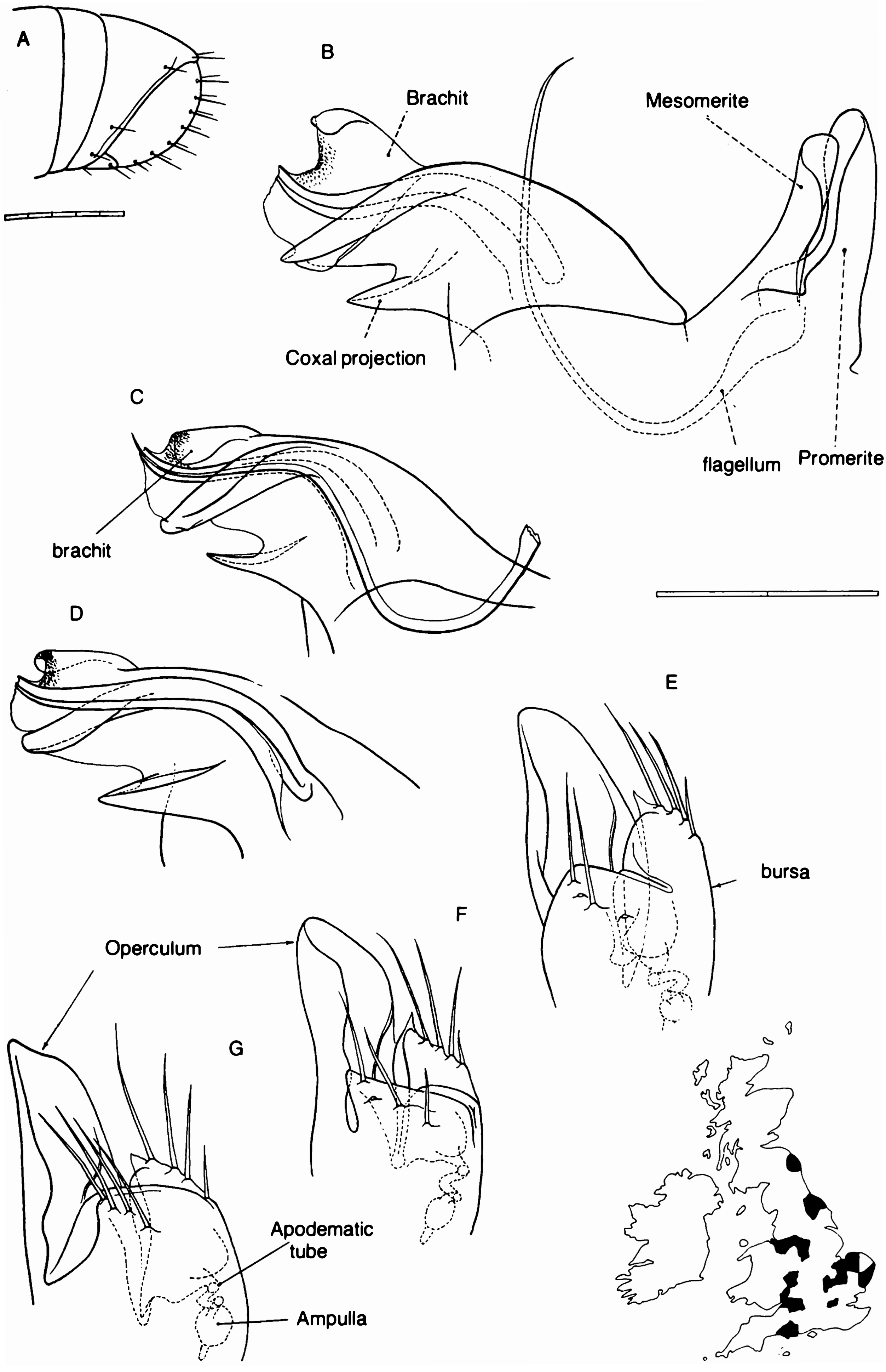
More weakly pigmented than the otherwise similar *C. latestriatus* and *C. britannicus.* Rich red ozadenes like those of *britannicus* give the overall appearance of pale lilac although some individuals are light brown. Adults may be recognized by more than five pairs of setae on the anal valves compared with three pairs in *latestriatus* and *britannicus* and usually seven or more in *C. truncorum.*

Distribution

British Isles: The first occurrence of this species in Britain was in sandy soil at Nantwich in Cheshire associated with *C. latestriatus*; both species were included under the last name by Curtis (1845). It was first knowingly recorded from under bark of an old tree stump near the churchyard of Upper Arley in Worcestershire (Brade-Birks, 1918d). The species was not reported for 33 years when Mr. J. H. Halliday found it in an old tree trunk lying in the 'Wilderness' at Marlborough College, Wiltshire in July 1951 (see Blower, 1953). Four years later I found a large poulation in a sawdust dump, the product of war-time timber operations near Byeland Abbey in the North Riding of Yorkshire. Later from rotten stumps in the grounds of March Grammar School, Cambridge (Langton, 1968) and from slowly decomposing leaf litter in Chelsea Physic Garden, London (Davis, 1982). Most recently the Survey has added records from west Norfolk, Bedford, Derbyshire and Cheviotland. Barber has the species from Dorset, and Read from Gloucestershire (VC34).

Europe: The species appears to be equally rare on the continent; it was first described from the catacombs in Paris and has been since recorded on one or two occasions from France, Holland, Belgium, Denmark, Germany, Austria, Yugoslavia, Czechoslovakia and the USSR, from gardens, greenhouses, graveyards and similar places associated with human activity.

Fig. 50. *Cylindroiulus parisiorum.* A. Tail end to show absence of caudal projection and more than five pairs of setae on the anal valves; B. External profile of left gonopods; C. Internal profile of opisthomerite of right gonopod; D. External profile of opisthomerite of left gonopod; compare with B in which the brachit is more open due to coverslip pressure; E–G. Posterior and posterolateral views of left vulva.


A
B
Brachit
Mesomerite
Coxal projection
flagellum
Promerite
C
brachit
D
E
bursa
F
Operculum
G
Apodematic tube
Ampulla

Cylindroiulus truncorum (Silvestri)

(Fig. 51)

Diploiulus truncorum Silvestri, 1896: *Il Naturalista Siciliano 1*: 160–161,
pl. 17, Figs. 11–13

Male	VIII	(31)36–42(44)	Length: 10.7–16.9 mm	Diameter: 0.81–1.13 mm
Female	VIII & IX	(31)38, 39(45)	(11)13.2–14.8(17)	(1.0)1.11–1.23(1.15)

Measurements of 8 males and 3 females from Kew
Bracketed figures from Schubart (1934)

Brown to almost black with bright red ozadenes as in *britannicus* (p. 158) and *parisiorum* (p. 160) more evident in younger animals. Amongst the tailless British species of *Cylindroiulus* '*luscus*'-group only the largest females of *C. latestriatus* (p. 155) develop the depth of pigment shown by most of the *truncorum* from Kew. Females and some of the males have widely spaced metazonite striae like the other 'latestriate' species but some males (five of the nine from Kew) have deeper, more numerous flutings on the metazonites which give the animal a characteristic glistening appearance. Anal valves with at least seven setae on one side, up to twelve, and rarely the same number on both valves.

Females of *truncorum* are similar in size to *latestriatus* and *britannicus* but the range of size in the males extends beyond the upper limits set for these two latter species. *C. truncorum* appears to mature with a similar number of segments to *latestriatus* and *britannicus*, but *truncorum* has from four (females) to seven (males) extra segments at the upper end of the range. By inference from what is known of the life-histories of closely related species it appears that *truncorum* is more inclined to mature in stadia VIII and IX than *latestriatus* and *parisiorum* which mature mainly in stadia VII and VIII.

Distribution

British Isles: First reported from Britain by Lindroth (1957) on the authority of a personal communication from Professor Ernst Palmen, from near Bristol. The first example of this species in British hands was found by Dr. Rundle on peat, in hothouses at the Royal Botanic Gardens, Kew, in December 1975 and later in three other houses in 1976 and also outdoors by the ruined arch and in moist leaf litter in the grounds. In both indoor and outdoor sites at Kew, the species was associated with *C. britannicus*.

Europe: According to Schubart (1934), probably introduced into northern Europe from the Mediterranean quite recently. Palmen noted the absence of records of the species from Finland until 1945 yet much material had been worked before this. Sweden, Belgium, Holland, Denmark, and Switzerland, France, Germany, Poland.

Probably indigenous in North Africa (Tunisia, Algeria). Introduced into the USA and Brazil.

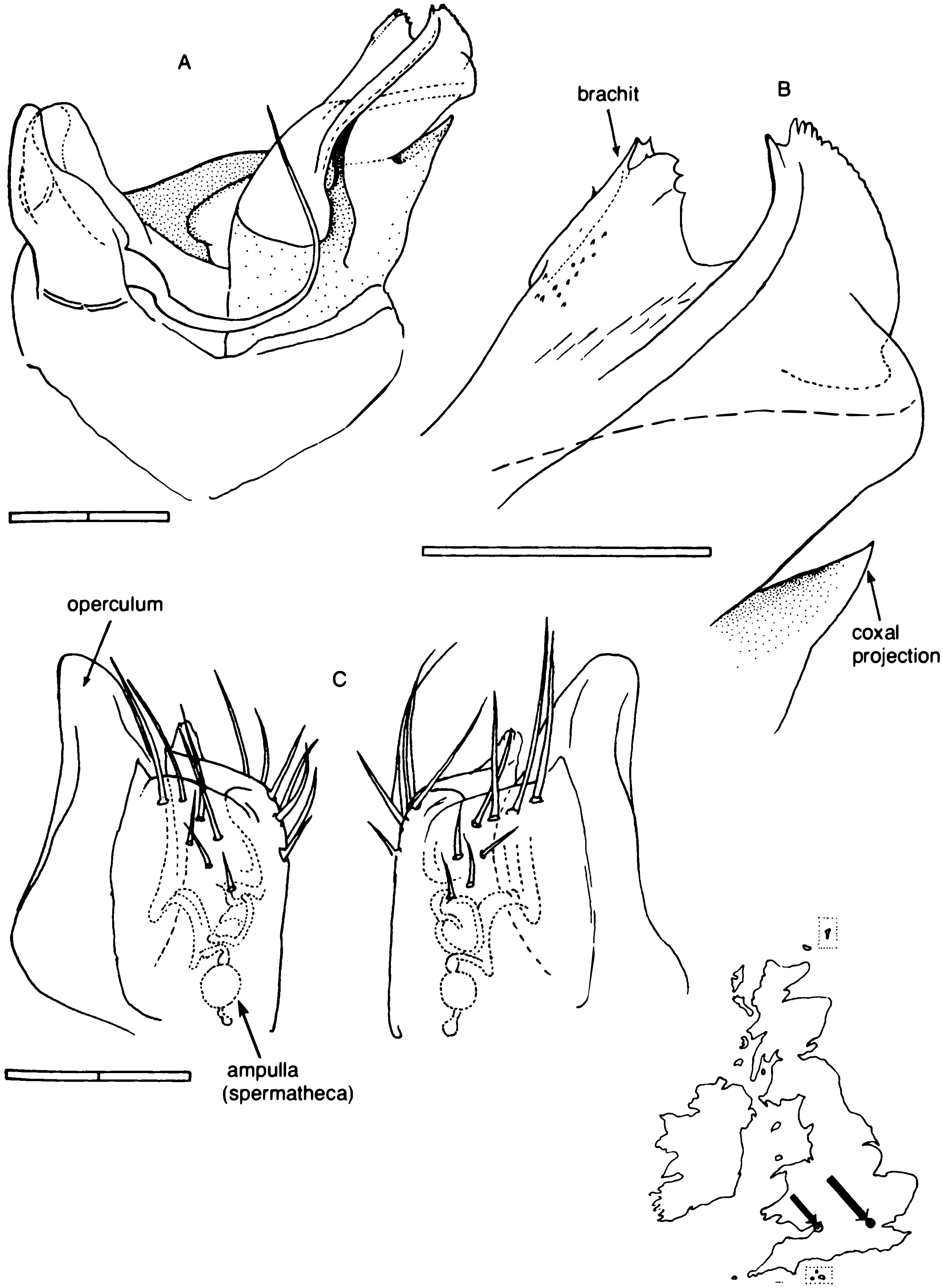


Fig. 51. *Cylindroiulus truncorum*. A. Internal view of left gonpods; B. Enlarged view of apex of opisthomerite; C. Right and left vulvae of same female, posterior view.

Enantiulus armatus (Ribaut)
(Fig. 52)

Leptophyllum armatum Ribaut, 1909: *Bull. soc. d'Hist. nat. Toulouse* *43*: 144–147, Figs. 1–3

Male	35–48	Length: 8.8–12.6 mm	Diameter: 0.63–0.87 mm
Immature Male	28–31	6.6–7.6	0.65–0.72
Female	40–51	9.3–15.1	0.78–1.05
Immature Female	36–38	8.4–9.3	0.72–0.78

Ribaut gives (38) 40–67 segments, males, 9–19 mm × 0.5–1.00 mm, females 'a little more robust'.

The British examples appear to mature with a similar size and number of segments to those from France, but do not proceed as far over the range of size and segment number.

The animals have very little epidermal pigment; in life they appear light olive green due to the gut contents modifying the light amber colour of the outer layers of the cuticle and thus are rather similar to *Cylindroiulus nitidus* (p. 150). This similarity to *C. nitidus* includes the slightly ventrally directed caudal projection, but the distinctive field character of *E. armatus* is the unusually long and slender anal scale 'detaching itself from the anal valves along half its length' (quoting from Ribaut's description). The ocelli are ill-defined and I have found it quite impossible to determine the stadium of an animal by reference to the ocular field.

Distribution

British Isles: First found in Britain by Dr. E. H. Eason, in superficial soil and litter layers of a mixed deciduous wood with beech, ash, hazel and elder at Salcombe Hill, near Sidmouth, south Devon, and from Sidmouth golf links, May, 1958. Nine years later I found the species in the northern tip of Great Haldon forest in a deep accumulation of beech leaves in a depression by the forest ride flanked by rhododendrons, April 1967.

Europe: Only known from the type locality, in dead leaves in the forest neighbouring Cayroulet and Hautaniboul, north west of the Montagne Noire.

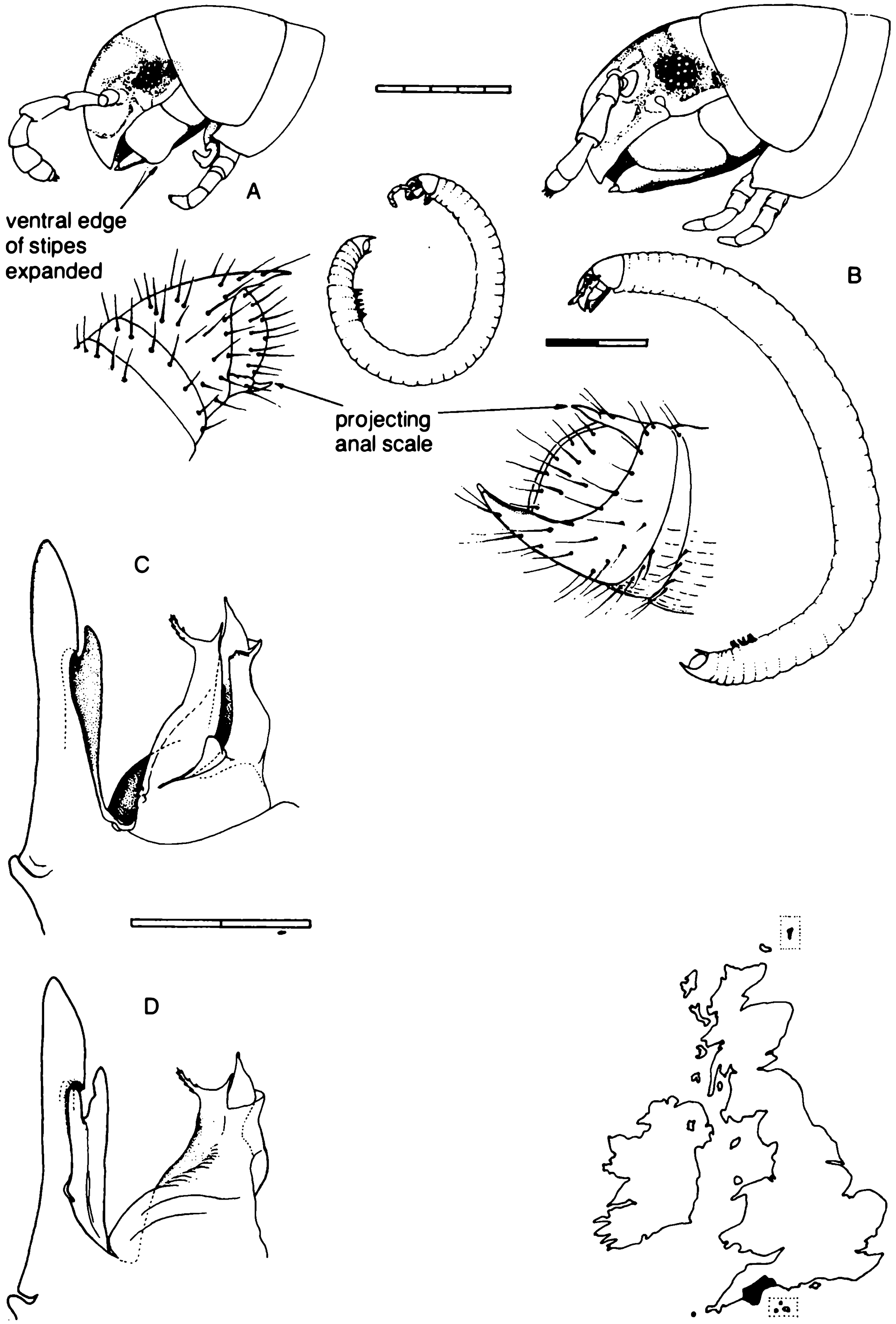


Fig. 52. *Enantiulus armatus.* A. Outline drawing of male with enlarged views of head and tail; B. Outline of female with enlarged views of head and tail. In A and B note the irregular arrangement of the ocelli; it is not possible to discern the separate increments of ocelli added at each moult. Note also the unusual ventral scale projecting beyond the anal valves. C. Internal profile; D. External profile of the gonopods; note the absence of a flagellum.

Tribe JULINI

Long slender julids with ozopores a short distance posterior to the suture between pro- and metazonite. Fringing setae on the metazonites prominent. Pre-anal ring and anal valves highly setose; telson produced into a long pointed caudal projection. With normal crochet-form first legs in the male (*Leptoiulus*, p. 176–9) or rather long and scythe-shaped (*Ophyiulus*, p. 172) or with very reduced first pair (*Julus*, p. 168). Cardines of male not expanded. British species without adhesive pads on legs of males. Opisthomerites of *Leptoiulus* and *Ophyiulus* with postero-lateral phylacum and anterior velum. Gonopods and second pair of legs of male *Julus* wholly distinctive.

It is usual to place *Julus* in the tribe Julini and *Ophyiulus* together with *Leptoiulus* in a separate tribe Leptoiulini. Certainly *Julus* stands apart from the other three genera in regard to the structure of the secondary sexual characters, but I have retained all three genera in the tribe Julini in the older and wider sense, to emphasize their biological similarity, especially that between *Ophyiulus pilosus* and *Julus scandinavius*; these species are unusual among the julids in remaining inactive in the nest as stadium II, and not leaving the brood until stadium III to take up food (Fig. 7). In Britain, both species develop up to stadium VI and VII by their first winter; males mature at stadium IX or X, although maturation occurs at the end of two years in *O. pilosus* and three years in *J. scandinavius*. Both species do not undergo further moults after first achieving maturity. *Leptoiulus* spp. may have similar life histories but there is insufficient data for British species so far. Demange (1981) retains *Julus* along with *Ophyiulus* and *Leptoiulus* in the same group which he elevates to a sub-family.

Julus scandinavius and *Ophyiulus pilosus* are two of our commonest snake millipedes; they are very similar in appearance; adult females are difficult to tell apart; they have identical caudal projections (Fig. 39c). Our two species of *Leptoiulus*, *L. belgicus* and *L. kervillei*, are not so common, but in the south *kervillei* coexists with *J. scandinavius* and *O. pilosus*, and in the south west *L. belgicus* may also be present. All four species have identical caudal projections. Many of the immature stadia of *O. pilosus* and *J. scandinavius* may be separated by counting the podous segments and rows of ocelli and referring to Fig. 9. Adult males are easily determined (see Figs. 1, 53). Adult females of *L. belgicus* may be recognized by the dorso-median light stripe, but females of *O. pilosus*, *J. scandinavius* and *L. kervillei* are more difficult. Reference to Table 3 will help in diagnosis using data of stadium, number of podous segments and size. Vulvae (Figs. 53, 54, 56) may be useful as a final check.

Table 3 *Statistics for female Julini*

	Julus scandinavius			*Leptoiulus belgicus*		
	podous rings	length mm	diameter mm	podous rings	length mm	diameter mm
*IX	(40)41–44	15.1–21.1	1.38–1.88	41–45	17.9–18.9	1.44–1.62
X	(43)45–47(48)	19.6–28.0	1.94–2.34			
XI	(44)46–48(49)	22.5–30.5	2.23–2.71			
	Ophyiulus pilosus			*Leptoiulus kervillei*		
*IX	44–47(48)	14.0–18.1	1.24			
X	(47)48–51(52)	19.6–29.5	1.50–2.06	44–53	15.2–16.8	0.99–1.13
XI	51–54(56)	26.6–29.3	1.85–2.17			
XI	56	29.0	2.03			

J. scandinavius has fewer podous rings in stadia X and XI than the corresponding stadia of *O. pilosus* with very little overlap at X and none at XI.

* No females mature in stadium IX in *J. scandinavius* or *O. pilosus*.

Bracketed figures in less than 5 individuals.

L. belgicus mature at stadium IX with similar number of rings and size to *J. scandinavius*. Adult *L. belgicus* therefore always with fewer rings, shorter and thinner than *Julus scandinavius*.

L. kervillei mature at stadium X with similar number of rings to *O. pilosus* but are much shorter and thinner than *O. pilosus* at X.

L. kervillei has more rings than *belgicus* but is shorter (no overlap) and thinner (no overlap).

Julus scandinavius Latzel

(Figs. 2, 7, 10 and 53)

Julus scandinavius Latzel, 1884: *Die Myr. der Ost-ung. Mon.*, *2*: 322–325

Sexual dimorphism at stadium VII

Male	IX–XI	(39)40–47(48)	Length: 13.1–24.3 mm	Diameter: 1.35–1.95 mm
Female	X, XI (XII)	45–48(49)	19.6–30.5	1.94–2.71

Bracketed figures exceptional

Schubart's lengths greater but diameters similar; three or four segments extra at upper end of the range of his animals.

Adults sometimes quite black like *Ophyiulus pilosus* (p. 172; Fig. 54) or *Tachypodoiulus niger* (p. 135) but never with contrasting white legs as in the latter; often less black, brown-black or even oily brown. The pigment not lightened by conspicuous mottling laterally and ventro-laterally as in *O. pilosus*. Immature stadia lighter brown with darker brown ozadenes and darkening around them which, together with a median dorsal line recalls the *Ommatoiulus* (p. 131; Fig. 41) pattern.

The metazonites are 'scored' with longitudinal striae rather than fluted like *O. pilosus* and the fringing setae in mid-trunk region usually much shorter than the length of the metazonite; the animals are less obviously pilose than *O. pilosus*.

Adult males are readily recognizable by the mesial ventrally directed coxal processes of the second pair of legs; the first pair are so reduced and atypical as to be invisible in a casual lateral view (there appear to be only six pairs of legs anterior to the gonopodial gap). Adult females and immature stadia are less easily separable from those of *O. pilosus*; reference to the table of anamorphosis may help or the vulvae may need examining. Special care must be exercised with females and immature stadia from the south which may belong to *Leptoiulus* spp (p. 176–9).

Biology. Mating has been described by Haacker (1969b). Sexes approach each other, meet head-on and walk up each other's ventral surface for a short distance juxtaposing gonopods and vulvae. The female takes the coxal processes of the second pair of legs in her jaws; males may often be found lacking the apical half to two-thirds of these processes after pairing. As in *O. pilosus*, but unlike most other julids, the first two stadia do not leave the nest and the stadium III is the first to leave the brood and take up food. Blower (1979) describes the post-embryonic development and life cycle of this species in a Cheshire wood. Here, as probably elsewhere in Britain, it is a semelparous triennial (that is, females take three years to reach maturity and die after breeding). Eggs laid in the spring reach stadia VI or VII by their first winter, stadia VIII and IX by the second and adulthood by the third; males in stadia IX and X, females in stadia X or XI. Three year old adults breed in the spring and die; there are thus very few adults around in late summer. Although there is only one breeding season, Mr. Davidson

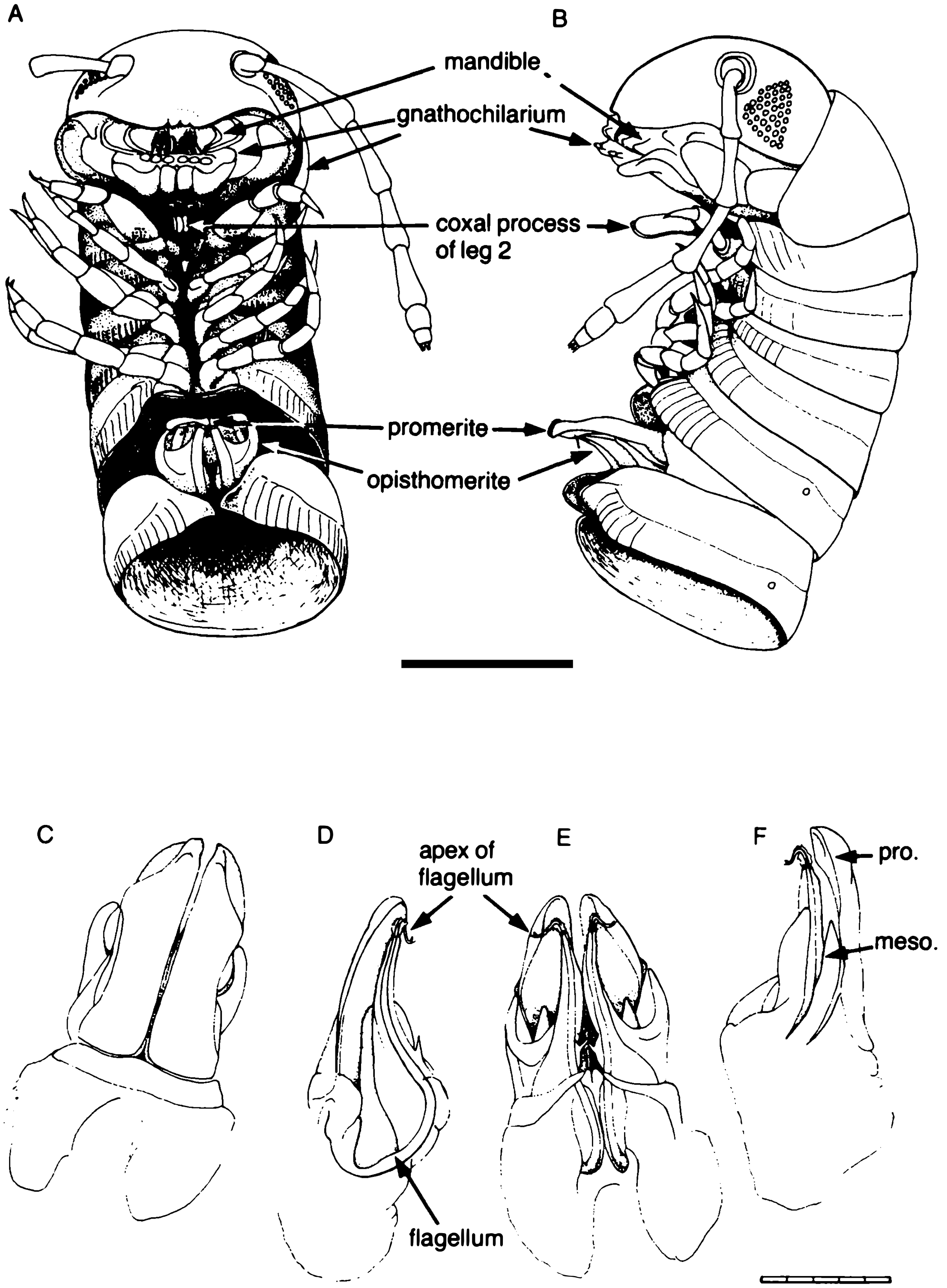


Fig. 53i. *Julus scandinavius*. A. Head and anterior seven rings of a stadium X male in ventral view; B. Lateral view of same; in A and B the seventh ring has been slightly displaced away from the remainder to expose more of the gonopods; C–F. Gonopods viewed in different positions; C. Anterior view; D. Internal profile of left gonopods; E. Posterior; F. External view.

has reared animals in the laboratory which have laid up to four successive broods. Overwintering densities in the Cheshire wood referred to above average 40–60 per m^2 with relative proportions of one, two and three year old animals of 4:2:1.

Distribution

British Isles: First recorded in Britain by Leach (1815) as *Julus terrestris* Linné. The true *J. terrestris* Porat does not occur in Britain, but up to the turn of the century the name was probably given to any of the large black/black-brown tailed julids. *Julus scandinavius* is the ninth most frequently recorded species in Britain. Unlike gaps in the map of *O. pilosus*, the gaps in the records for *Julus* cannot be accounted for entirely by the paucity of collectors; it is not recorded for Sussex south (VC13), east (VC14) or Gloucester east (VC33) which are well-worked vice-counties; Kime (1978) has it ranked 23rd in his survey of Surrey, Sussex and Hampshire compared with its rank for England overall in Blower (1972) of tenth and comments that he found it in only two of the 198 Km squares he examined in the south east, both on a Surrey heath. In the north it occurs in most areas of deciduous woodland with a reasonable cover of litter, but is never so numerous as *O. pilosus*. It has a preference for more acid sites where it is associated with *Cylindroiulus punctatus* (p. 152). On less acid soils it is sometimes associated with *O. pilosus* (hence diagnostic difficulties). The intriguing details of the association or disassociation of *J. scandinavius* and *O. pilosus* are discussed by Miller (1974). *J. scandinavius* occasionally occurs in open land, especially on the coast where it is characteristic of older dunes and coastal plantations; it is rarely found in cultivated land.

Europe: Widespread on the continent except in Finland in the north, Italy and Yugoslavia in the south, Spain and Portugal in the south west, and Romania and Bulgaria in the East; absent also from the European plain of USSR but recorded from the Carpathians.

Introduced into the USA (Jeekel, 1973).

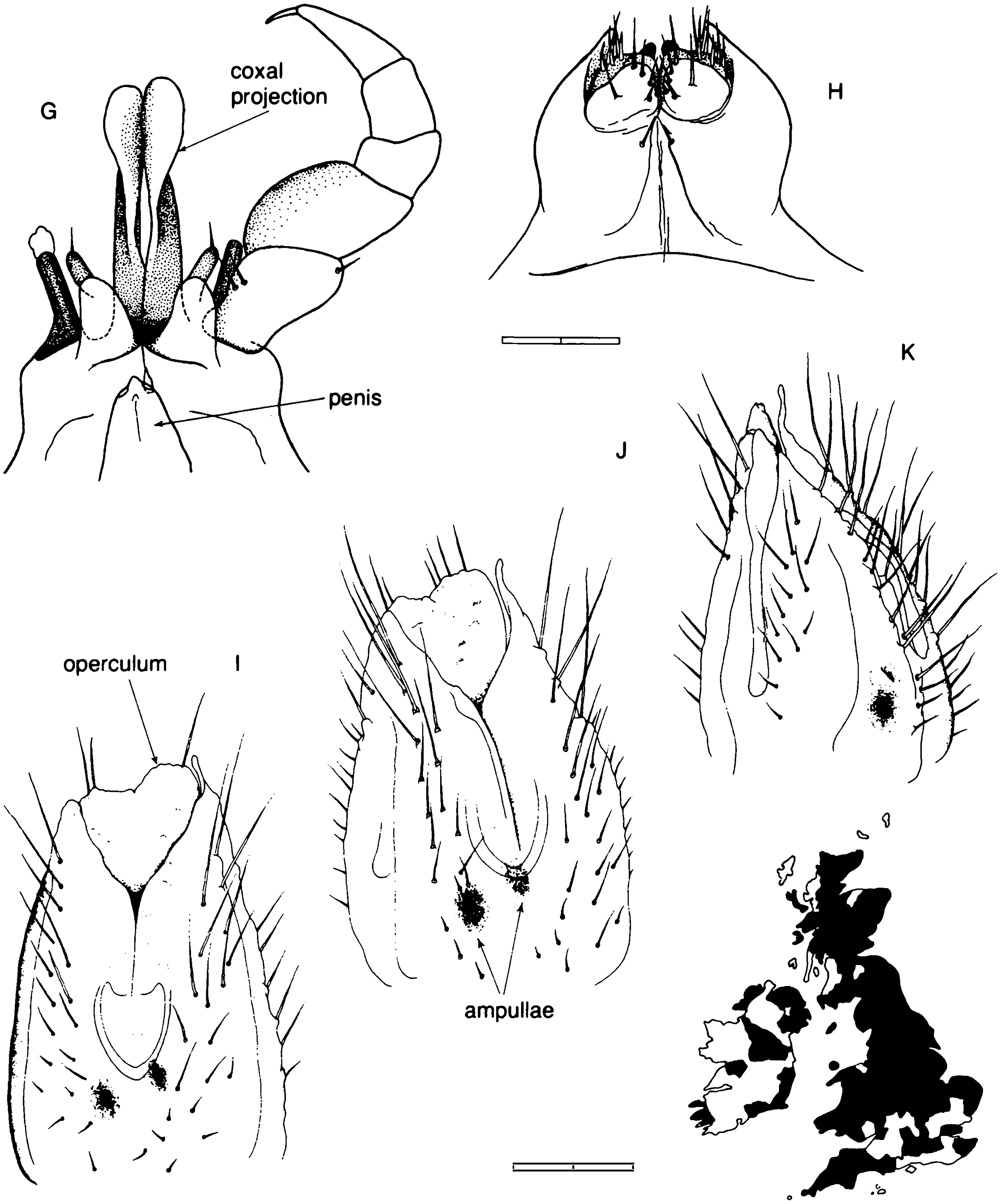


Fig. 53ii. *Julus scandinavius*. G. Posterior view of the second pair of legs of the male with median coxal projections and penis behind; H. First pair of legs of the male from behind; I–K. Views of the left vulva, drawn to same scale and in similar positions to those in Figs. 54 C, D and E, for direct comparison. I. posterior view; J. posterolateral; K. Lateral view.

Ophyiulus pilosus (Newport)
(Figs. 1 and 54)

Julus pilosus Newport, 1842: *Proc. ent. Soc.*, 2 May *1842*; *Ann. Mag. nat. Hist.*, (1) *11.*, 316 (1843)
Ophyiulus fallax Meinert of continental authors

Sexual dimorphism at stadium VII

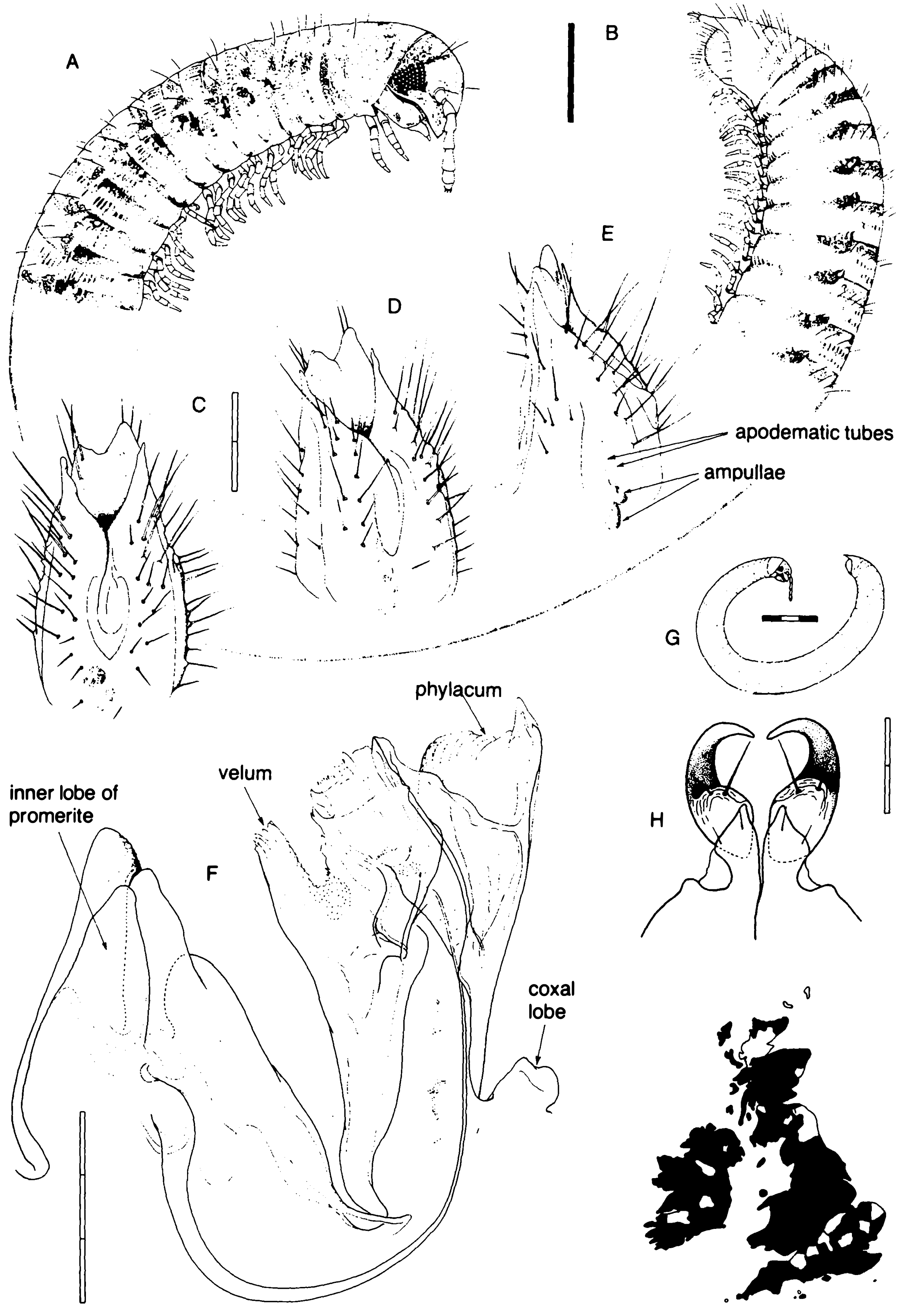
			Length:	Diameter:
Male	IX–XI	(42, 43)44–51(54)	13.8–19.4(21) mm	1.03–1.10(1.14) mm
Female	X–XI(XII)	(47)48–54(56)	19.6–29.3(30) mm	1.50–2.17 mm

Bracketed figures exceptional, the higher numbers of podous segments and dimensions refer to examples from Dorset and Sussex sent to me by Mr. Kime. Schubart (1934) gives even larger numbers of podous segments and lengths but these belong to an alpine race *major*. The majority of British individuals have, stadium for stadium, more segments and smaller diameter than *Julus scandinavius* (p. 168).

Adults quite black or brown-black but never with contrasted white legs as in *Tachypodoiulus niger* (p. 135). Laterally and ventro-laterally the prozonites are lightened by discrete mottlings caused by the absence of dermal pigment over the muscle attachments. Metazonites fluted like a Doric pillar and fringed with conspicuously long setae attaining anteriorly and posteriorly at least, the full length of the metazonite (hence the trivial name *pilosus*). Immature stadia noticeably ligher brown, still conspicuously mottled and with rich blood red ozadenes recalling the colour of those of *Blaniulus guttulatus* (p. 116) and *C. britannicus* (p. 158); immatures are overall similar in colour to this last named species.

Adult males are readily recognizable by the well developed sickle-shaped first legs and the ventrally swollen gnathochilarium. Adult females are less easy to separate from those of *Julus scandinavius*. The metazonite sculptor and the setation are helpful indications – with some practice. Certainty of diagnosis of live specimens can be achieved by viewing walking animals from above: in this species the legs are hardly discernible and do not appear to

Fig. 54. *Ophyiulus pilosus.* A, B. A female at stadium IX (eight rows of ocelli), the stadium just before adult. A. Detail of the first fifteen rings to show pigmentation; B. The last nine podous, three apodous rings and telson; the light spots, mid lateral (more evident in B), are the ducts from the ozadenes, not the ozopores; C, D and E. Posterior, posterolateral and lateral views of the left vulva, drawn to the same scale and in similar positions to those of *Julus scandinavius* (Figs. 53, I, J and K), for direct comparison; F. Inner profile of left gonopod; G. Same animal as A and B drawn to the same scale as stadium IX of *Leptoiulus belgicus* (Fig. 55C), and *Leptoiulus kervillei* (Fig. 56A); H. First pair of legs of male, posterior view. See also Fig. 1.


A
B
E
D
C
apodematic tubes
ampullae
G
phylacum
velum
inner lobe of promerite
F
H
coxal lobe

protrude laterally whereas in *Julus scandinavius* they can be seen quite clearly (Davidson, pers. com.). For certainty of diagnosis of preserved specimens it is usually sufficient to determine the stadium from the ocular field and the number of podous segments, and then refer to Fig. 9 (p. 21) and Table 3 (p. 167). In the eventuality of overlap of a number of podous segments the vulvae must be examined. Immature stadia can be determined by reference to Fig. 9 but care must be exercised with females and immatures if the animals come from the south where either of the two species of *Leptoiulus* (p. 176–9) might occur.

Biology. This species can progress on occasion by rapid flexion of the body in a snake-like manner (hence the generic name). The many segments and conspicuous flexor muscles attaching vento-laterally may be associated with this ability. As in *Julus scandinavius*, the first and second stadia stay within the nest; the third stadia are the first to wander abroad and feed independently. Blower & Miller (1974) give details of the anamorphosis and life-cycle of this species from several sites in north and south. The species is a semelparous biennial. Eggs laid in the spring develop to stadia VI or VII by their first winter and to adults by the second winter. Maturity is achieved by males in stadia IX or X (rarely XI) and by females in stadia X or XI (rarely XII). These two-year old adults lay eggs and then die; there are thus very few adults around in late summer. Although there is only one breeding season, up to four broods from individual females have been obtained in the Laboratory (Davidson, pers. com.). In a south Wales oak wood Blower & Miller (1974) record overwintering densities of 200–530 individuals per square metre, 80–90% of which belong to stadia (V) VI and VII. Mating is described by Blower (1974a) and is similar to the process described for *J. scandinavius* by Haacker (1969b).

Distribution

British Isles: First recorded and described by Newport (1844). Now the second most frequently recorded species in Britain; the gaps in the vice-county distribution corresponding with the poorly-worked areas. A characteristic inhabitant of deciduous woodland reaching high densities. It is often associated with *Julus scandinavius* but is usually the dominant member of the association on moderate to base rich soils. Unlike *J. scandinavius* it is often frequent in gardens and in and around farmland; it is more inclined to exploit dead vegetation associated with human activity, i.e. it is more synanthropic which may account for its introduction to distant countries.

Europe: Throughout most of the continent with the noteable exceptions of France, Belgium and Finland. Unlike *J. scandinavius* it occurs south to Northern Italy and Yugoslavia and also in both the European plain and Carpathian regions of the Soviet Union.

It has been introduced and become established in the eastern parts of Canada and USA (from Nova Scotia and Quebec, south to Virginia and Tenessee), and in New Zealand.

Leptoiulus belgicus (Latzel)
(Fig. 55)

Julus belgicus Latzel, 1844: *Bull. Soc. Ent. Belg.*, *28*: 249, one figure

Male	IX	41–44	Length: 13.8, 16.8 mm	Diameter: 1.15, 1.18 mm
Female	IX	41–45	17.9–18.9	1.44–1.62

Measurements of two males and four females from near Falmouth. Lengths from Schubart (1934) are greater than, and outside the range of those above. Schubart's numbers of podous segments are similarly greater. Possibly the German individuals mature a stadium later than here in Britain but the diameters he gives are very similar to those given above.

Dorsally the trunk is brown to dark brown with a quite distinctive median dorsal pale yellowish-white line. Metazonite setae one quarter to one fifth the length of the metazonite in the mid trunk region, longer towards head and tail, attaining half to two thirds the length of the metazonite on the last few rings.

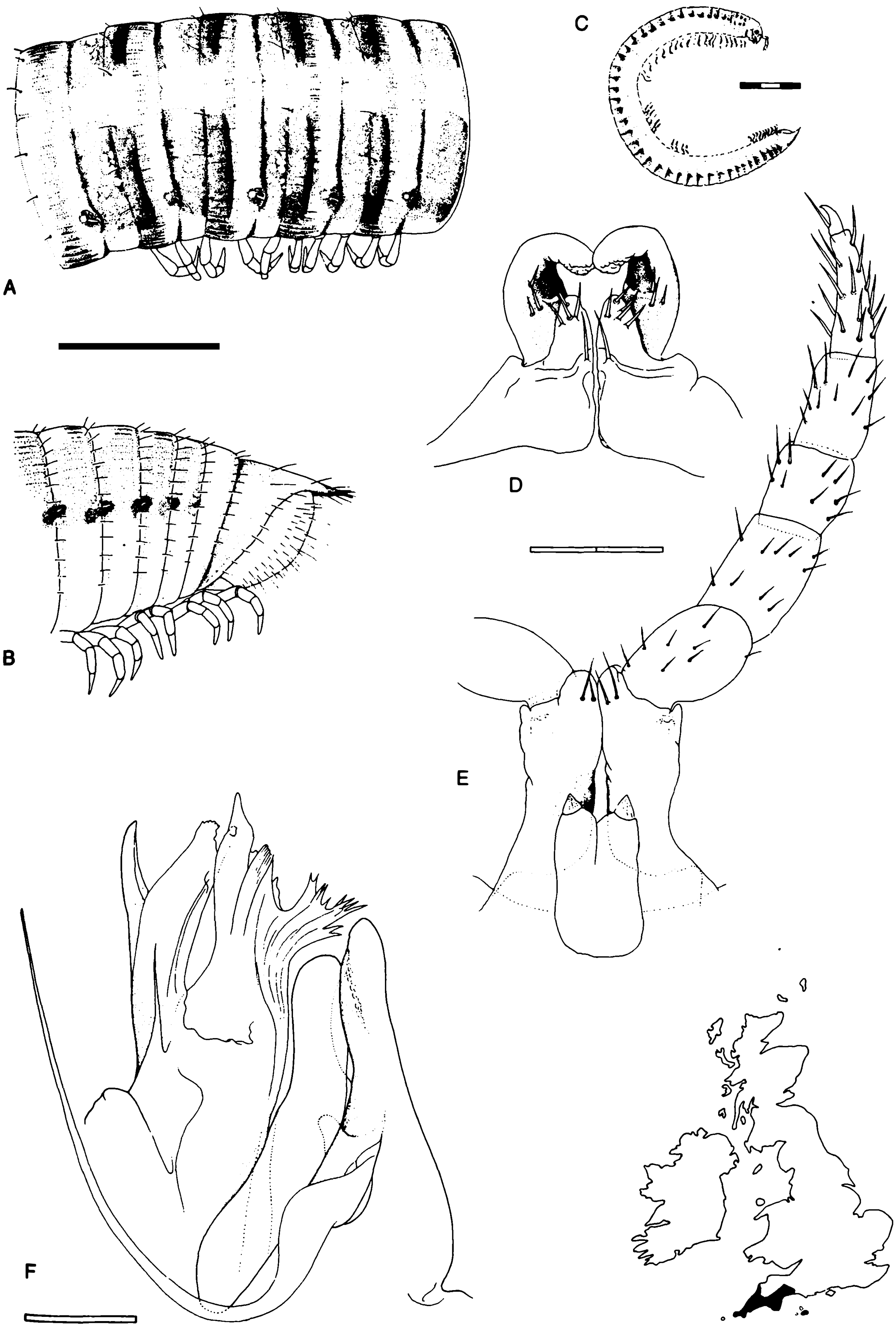
Adult males have the usual crochet-formed first legs (*cf.* the exceptional character of those of *Ophyiulus pilosus* (p. 172) and *Julus scandinavius* p. 168)) and coxal projection from the second pair is absent (*cf.* the distinctive projections in *Leptoiulus kervillei*, p. 178). Adult females possess the same distinctive dorso-median light line as the males. Young stadia may easily be confused with the other julines.

Distribution

British Isles: First recorded by Bagnall (1922) from Torquay, south Devon (VC3) in bracken and coniferous litter. Next found in west Cornwall (VC1) in litter by Turk (1944) and from east Cornwall (VC2) by Blower at Trelill by Camelford in 1961. Most recently from Devon (VC3), near Plymouth (R. Daniel); Falmouth (S. J. Fear), and Two Waters Foot (A. D. Barber), Cornwall (VC2). There is also a record from the Channel Isles.

Europe: Holland, Belgium, France, Germany, Switzerland and Austria. Also from Barcelona in northern Spain.

Fig. 55. *Leptoiulus belgicus.* A. Dorsolateral view, from right, of rings IX–XIII, slightly flexed in the vertical plane, to show the median dorsal light band; the metazonite of ring XIII on the left does not overlap the succeeding prozonite; the prozonite of ring IX on the right is not overlapped by the preceding metazonite; B. Tail end to show the straight (very slightly arcuate) hyaline apex; C. Small scale view of an adult female of stadium IX; same scale as the stadium IX *Ophyiulus pilosus* in Fig. 54G, and *Leptoiulus kervillei* in Fig. 56A; D. Posterior view of the first pair of legs of the male; E. Second pair of legs of male, without elaborations (compare with Fig. 56E), and penis behind; F. Internal profile of right gonopods.


A
B
C
D
E
F

Leptoiulus kervillei (Brolemann)
(Fig. 56)

Julus (*Leptoiulus*) *kervillei* Brolemann, 1896: *Feuille J. Natural.*, *26* (III), Nos. 306 & 307, pp. 118–119 & 133–134, Figs. 1 & 2

Males	IX, X	(43)47–51	Length: 13.5–14.8 mm	Diameter: 0.74–0.92 mm
Females	X	(43)44–53	15.2–16.8	0.99–1.13

The animals described by Brolemann had more podous segments (50–58) and were longer and broader (24–25 × 1.3–1.4 mm).

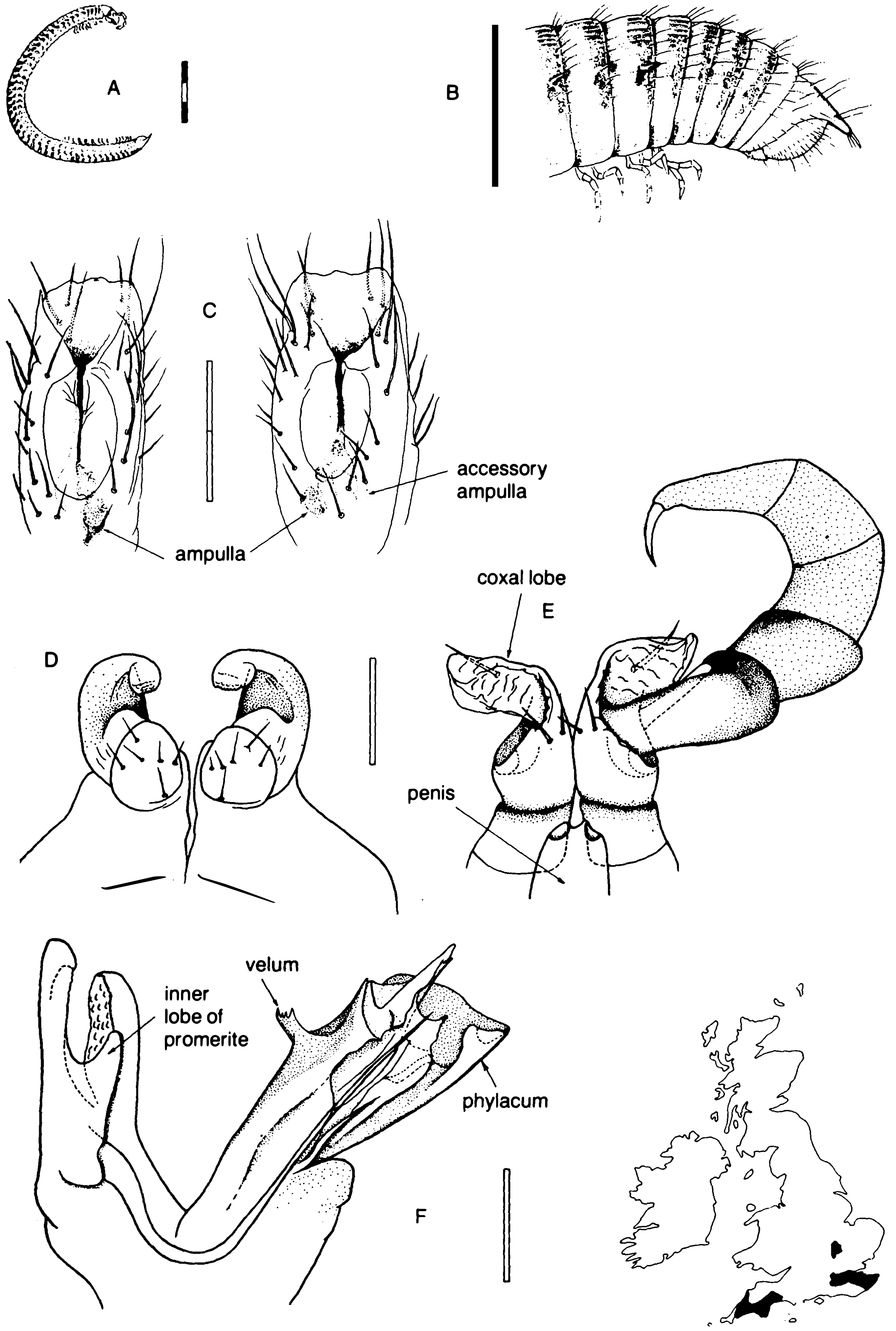
Ventrally pale, dorsally olive brown, mottled laterally in the manner of *Ophyiulus pilosus* (p. 172). Metazonites fluted, fringed with setae equal to half the length of the metazonite in mid-trunk region increasing to the full length of the metazonite towards head and tail. Adult males easily recognized by the characteristic coxal processes of the second pair of legs. Females and immature stadia easily confused with *O. pilosus*. Examination of the vulvae will confirm the identity of the adult females; immature stadia with similar numbers of podous segments but noticeably thinner than those of *O. pilosus*.

Distribution

British Isles: First recorded by Blower & Rolfe (1956) from East Kent, beneath chalk boulders in a disused chalk pit at Wye, 1934. Later found in West Kent, Meopham, and in south Devon, in beech litter at Ivybridge (May, 1972; Barber & Daniel, 1975) and from Cornwall, Denham Wood, near Buckland, Monachorum (June, 1972 and March, 1976). Most recently from Surrey and Bedford.

Europe: France. In his original description Brolemann (1896) includes material from Seine-et-Oise, Seine Maritime and Orne. Demange (1981) adds Marne and Mayenne. Also recorded from Holland and Belgium.

Fig. 56. *Leptoiulus kervillei.* A. Small scale view of IX stadium adult female; same scale as stadium IX females of *Ophyiulus pilosus* (Fig. 54G) and *Leptoiulus belgicus* (Fig. 55C); B. Tail end to show nearly straight hyaline apex of caudal projection; C. Left vulva (on right) and right vulva (on left) in posterior view; the left vulva has an aberrant accessory ampulla; D. First pair of legs of male from behind; E. Second pair of legs of male, posterior view showing characteristic coxal lobes and penis behind; F. Internal profile of left gonopods.


A
B
C
accessory ampulla
ampulla
D
coxal lobe
E
penis
velum
inner lobe of promerite
phylacum
F

Tribe METAIULINI

The single species occupying this tribe possesses Cylindroiuline-type gonopods; there is no flagellum or flagellum groove (absent also in *Enantiulus* (p. 164) among the Cylindroiulini). *Metaiulus pratensis* is blind and poorly pigmented (as *Cylindroiulus vulnerarius*, p. 147). On the other hand, *Metaiulus* has affinity with the Julini having ozopores lying well posterior to the suture between pro- and metazonite, and in the absence of expanded cardines in the male. Hoffman (1979) wonders whether its affinity with the Cylindroiulini may not justify its inclusion in that tribe; Demange (1981) includes *Metaiulus* in the Brachyiulini elevated to sub-family status.

Metaiulus pratensis Blower & Rolfe
(Fig. 57)

Metaiulus pratensis Blower & Rolfe, 1956: *Ann. Mag. nat. Hist.* (12) *9*: 513–519, Figs. 1–11

Male	26–43	Length: 7.2–13.5 mm	Diameter: 0.6–0.8 mm
Female	25–40	8.3–13.9	0.6–1.1

Without ocelli and without caudal projection, the only British julid with this combination. Almost without epidermal pigment; preserved specimens whitish to cream white with purplish-blue ozadenes standing out strikingly against the pale background colour. In life the animal presents a purplish-grey appearance.

Distribution

British Isles: First described by Blower & Rolfe (1956) from several localities in west and east Kent and one in Sussex. The animals were found mainly in heavy clay soils, at the roots of hops and also during the course of wireworm sampling of recently broken-up grassland.

Europe: The species was rediscovered in French caves to the south west of the Massif Central in the departments of Lot, Garonne and Tarn by Demange (1958, 1965) and Mauriès (1965). The French animals are regarded as three sub-species of the typical form.

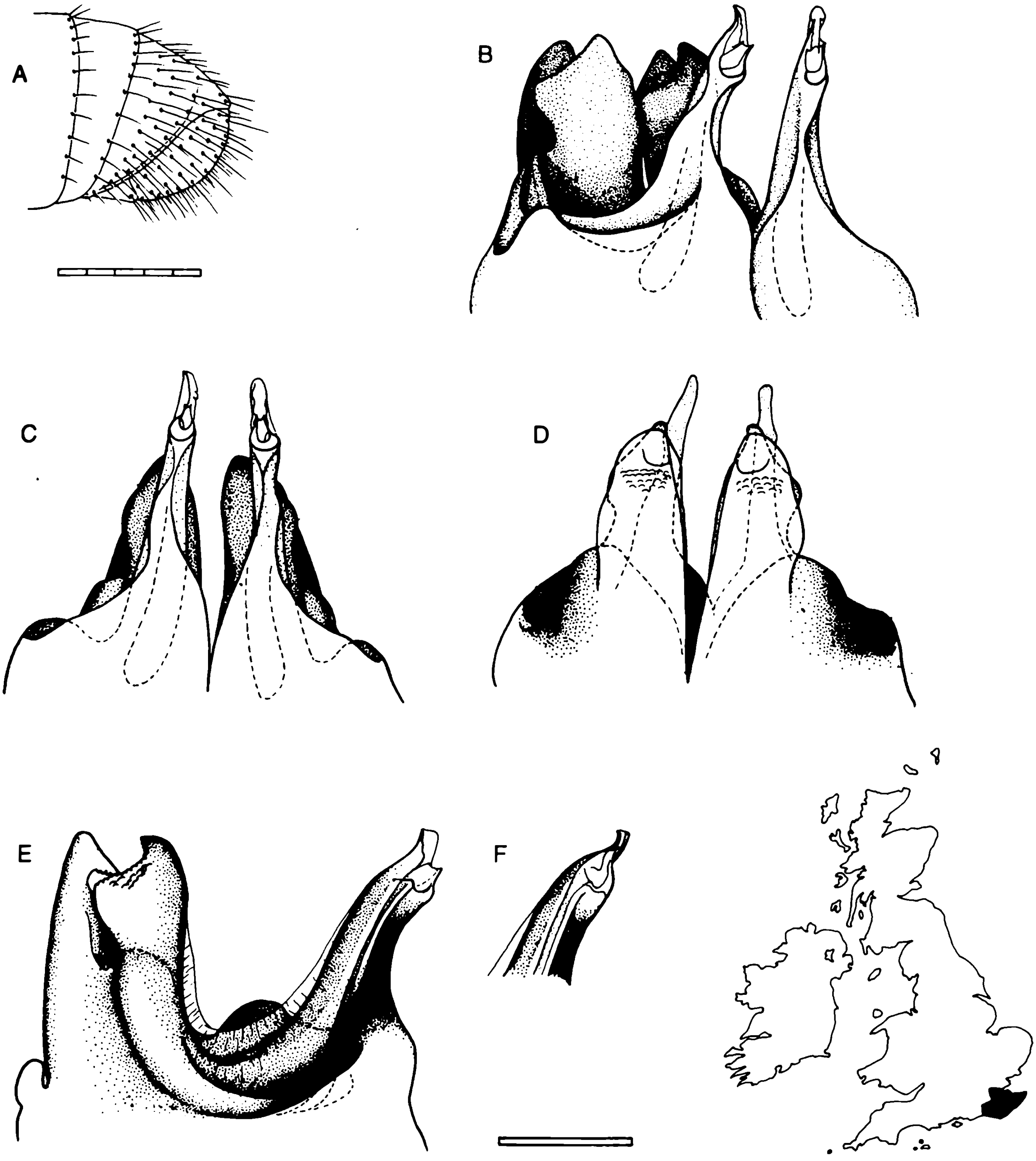


Fig. 57. *Metaiulus pratensis.* A. Tail end to show extensively setose preanal ring and anal valves; B–F. Different views of the Gonopods. B, posterolateral, C, posterior, D, anterior views; E. Internal profile of left gonopods; F, Apex of left opisthomerite, internal view, of a specimen mounted in euparal.

Tribe BRACHYIULINI

This tribe is characterized chiefly by the mesomerite of the gonopod retaining close relation with the opisthomerite and not associating with the promerite to give the pincer-like arrangement present in the other julid tribes. *Brachyiulus* (p. 183) is notable, as the generic name implies, for the small number of rings which go to make up the trunk. The cardines of the male are expanded and there is a flagellum. The metazonites are fringed with setae, the ozopore is on the suture between pro- and metazonite and the pre-anal ring is slightly produced into a barely discernible caudal projection. *Unciger* (p. 186) is characterized chiefly by a massive anteroventrally produced sub-anal scale; the mesomerite, whilst still retaining connection with the opisthomerite, opposes the promerite in pincer-like manner.

Brachyiulus pusillus (Leach)
(Fig. 58)

Julus pusillus Leach, 1815: *Trans. Linn. Soc. London*, *11* (2): 379
Brachyiulus littoralis Verhoeff, 1898 of continental authors

Sexual dimorphism at stadium V

Male	(VI?) VII	27–29(30)	Length: 7.2–7.6 mm	Diameter: 0.70–0.78 mm
Female	(VII?) VIII	(26)28–31	9.8–(13.0)	1.16–1.20

Figures in brackets from Schubart (1934)

Pattern of pigmentation very similar to that of *Ommatoiulus sabulosus* (p. 131) with two dorso-lateral light stripes along the trunk. The pigment is rather darker brown with less of a reddish tint than in *O. sabulosus* and the dorso-lateral stripes are a lighter yellow with less suggestion of orange. Adult *B. pusillus* are similar in size and have a similar pattern to stadia IV and V of *Tachypodoiulus niger* (p. 135), but in this last, the pattern is not so clear-cut.

The telson is only slightly produced but the animal, on first examination, appears tail-less. It is the shortest of our julids (hence the generic name). It matures early at stadia VII or VIII and there do not appear to be any further moults after maturity, it is probably a semelparous species. The gonopods of the male are unusual for a julid in being incompletely retracted within the body and remain protruding slightly.

Two of the individuals I have handled recently were gynandromorphs; a stadium VII from Reading had full-sized eggs, vulvae and immature gonopods; a stadium VIII from Gower, south Wales had vulvae and mature gonopods.

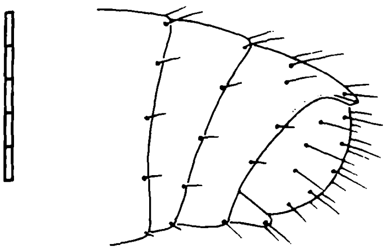
Distribution

British Isles: First recorded and described by Leach (1815) and now recorded widely throughout England, Wales and Scotland and in Northern Ireland. It is common in coastal habitats and also inland, usually in arable or grassland. It was found, for example, by Edwards (1929) in his survey of the fauna of grassland on boulder clay at Aberystwyth.

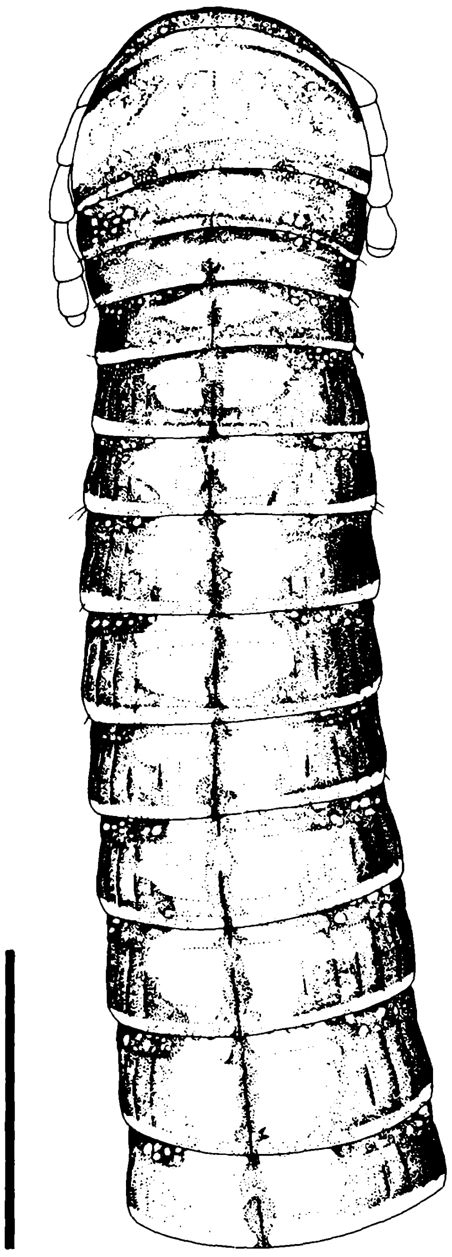
Europe: Recorded throughout Europe except Norway, Hungary and the Balkans (but present in USSR, on the European plain).

Introduced into the USA, occurring from New England south to North Carolina, inland into Ohio, Illinois and Indiana and from Mississippi in the south and California in the west; also from the Azores, Madeira, St. Helena, Tristan da Cunha, Argentine, S. Africa and Inacessible Island.

Fig. 58. ***Brachyiulus pusillus.*** A. Tail end to show slightly projecting apex of preanal ring; B. Dorsal view of the first thirteen rings to show the median dark band and the two paramedian yellow bands; C. Internal profile of left gonopods; the mesomerite is close to the opisthomerite and does not oppose the promerite to form the 'pincer' apparatus.



A



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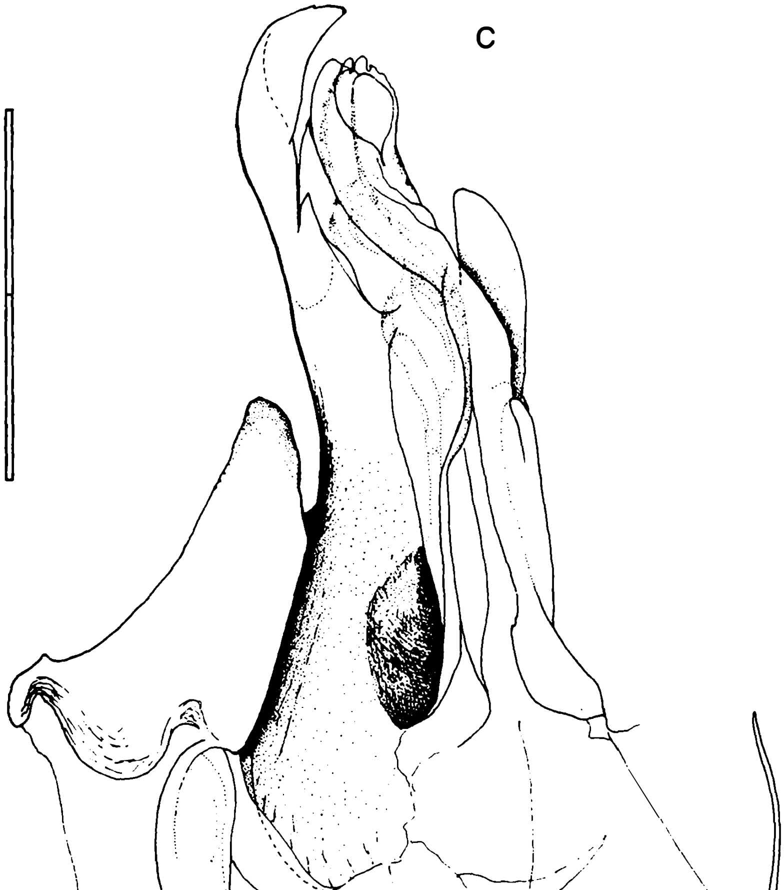


C

Unciger foetidus (C. L. Koch)
(Fig. 59)

Iulus foetidus C. L. Koch, 1838: *Deutschlands Crustaceen, Myriapoden*, p. 22, pl. 5

			Length:	Diameter:
Male	IX, X	(36)37, 38(39)	(20)21.9–27.3 mm	(1.2)1.60–1.67(1.8) mm
Female	IX, X	(37)38, 39(41)	(20)26.7–28.6	(1.6)2.04–2.33

Figures in brackets from Schubart (1934).

Dark brown to black, mottled with lighter patches due to muscle insertions. Metazonites vaulted (longitudinally) and with well-marked longitudinal flutings rather than striae. Setae fringing metazonites long and closely-set. Telson smoothly rounded, not produced, anal valves densely setose, sub-anal scale forwardly produced into an amber coloured scythe-like process extending beneath the last three rings.

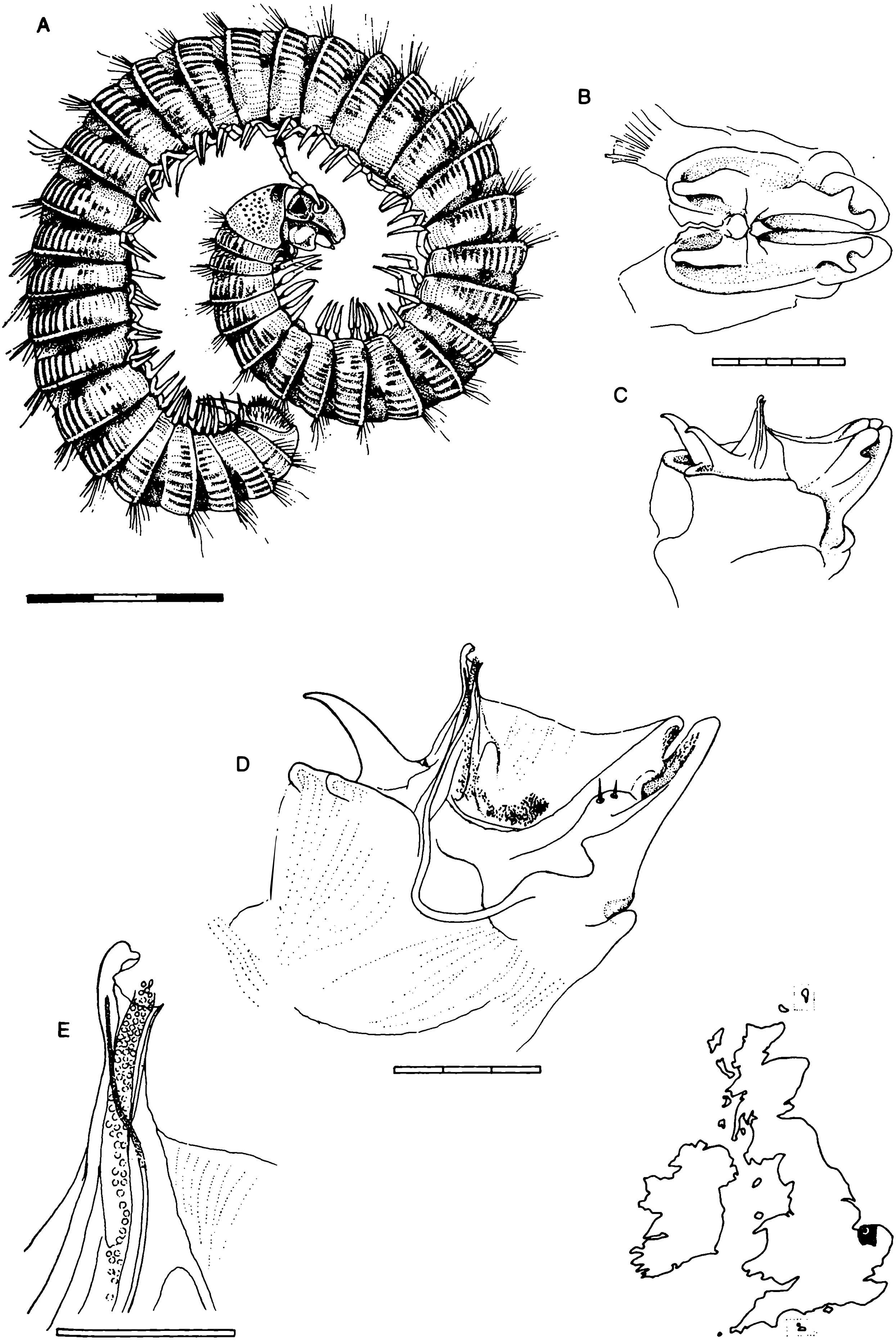
Biology. An account of a laboratory and field study of this species is given by Haacker (1970). Dr. Enghoff sent to me an interesting account of the post-embryonic development written one year after the species was described (Waga, 1839) which includes one of the earliest descriptions of the pupoid stadium of a julid.

Distribution

British Isles: The most recent addition to the British List, found by Mr. R. E. Jones of the King's Lynn Museum, in a garden at Dersingham, Norfolk, 27th April 1983. The dimensions given above come from three individuals of each sex; Mr. Jones has since seen further individuals in this same garden and is keeping them under close observation (Jones, 1985).

Europe: Norway, South Sweden, Holland, Denmark, Estonia, Latvia, Germany, North Italy (Dolomites), Austria, Czechoslovakia, Hungary, Yugoslavia, Romania, Albania, Poland, USSR (European Plain and Carpathians). The most recent record is that from Norway, near Bergen (Meidell, 1968). Meidell quotes Lohmander's suggestion that the species is native to East and Central Europe and has expanded to the West and North where it is distinctly synanthropic. In Denmark the species is able to live out-of-doors, but is probably introduced (Enghoff, 1974). Schubart (1934) records it mainly from open land (agricultural and park land) and as much more frequent on limestone.

Fig. 59. *Unciger foetidus*. A. Lateral view of a mature male with 37 + 1 rings. Note the forwardly produced anal scale partly obscured by terminal legs (compare with Fig. 40D); B, C. Ventral and lateral views of gonopods; D. Internal profile of right gonopods; E. Enlarged view of apex of solenomerite showing flagellum with bottle-brush setae, and sperm within the sperm channel.


A
B
C
D
E

Order POLYDESMIDA

Short-bodied, blind millipedes with flat or arched backs. The hinder part (metazonite) of each ring following the collum is produced dorso-laterally or laterally into keels called *paranota.* The trunk consists therefore of a series of wider flat or arched backs connected or bridged by the narrower prozonites, hence the ordinal name which means literally 'many bridges'.

The collum is narrower than the head and the succeeding (second) ring. All rings except the collum are closed ventrally; their sternites are fused with the pleuro-tergal arches to form complete cylinders. The sternites of the first and second pairs of legs are freely articulated in the ventral gaps in the second and third pleuro-tergal arches but the pleurites of these arches are united ventrally to form narrow bridges completing the ring. The coxae are inserted laterally and not close together as in the Julida (compare Figs. 4A and 4C). The legs are usually much stouter in the male.

Adults with 19 or 20 rings (telson included); immature stadia with 7, 9, 12, 15, 17, 18 and 19 rings. Ozopores on the lateral edges of the paranota except those of rings 6, 8 11 and 14 (in *Prosopodesmus panporus* (p. 190) ozopores are present on all the paranota of diplopodous rings).

There is a single pair of gonopods formed from the metamorphosed eighth pair of limbs (anterior pair of the seventh segment). The gonopod rudiments are present in all stadia from the third to the penultimate.

This is the largest order of Diplopoda, but in Britain it houses only the second largest group of species. It is divided by Hoffman (1979) into four sub-orders; British species are included in two of these. The sub-order PARADOXOSOMATIDEA, family Paradoxosomatidae, includes two species, *Oxidus gracilis* (p. 218) and *Stosatea italica* (p. 220); the remaining British species fall into three families of the sub-order POLYDESMIDEA; seven species in the Polydesmidae, two in the Macrosternodesmidae and one in the Haplodesmidae.

Key to the families of POLYDESMIDA

1. Flat-backed, paranota dorsolateral, with a characteristic pattern of tubercles (Fig. 64); medium sized to large animals, one species, *Brachydesmus superus*, with 19 rings in the adult, 8–10 × 0.8–1.0 mm, the rest (species of *Polydesmus*, with 20 rings, all over 10 mm long and 1.2 mm broad) .... Family POLYDESMIDAE (p. 192)

Arched-backed, paranota mid-lateral, with *either* smooth dorsal surface *or*, if tuberculate, small pale forms less than 5 mm long and 0.8 mm wide (Figs. 60, 68) **2**

2. Small species less than 5 mm long and 0.8 mm wide **3**

Medium to large species, adults over 10 mm long and 1.0–2.5 mm wide. Arched back with smooth dorsal surface, glabrous or with a few short setae along the anterior edge of the metazonites; moderately to well pigmented, amber to brown. Confined to hothouses or greenhouses – or to the south east of the country (Figs. 72, 73) .... Family PARADOXOSOMATIDAE (p. 216)

3. Ring II wider than the following, with paranota directed ventroanteriorly to embrace the collum. Ozopores on all diplopodous rings (Fig. 60) .... Family HAPLODESMIDAE (p. 189)

Ring II not wider than the following, ozopores in normal interupted sequence (Figs. 69, 70, 71) .... Family MACROSTERNODESMIDAE (p. 209) and *Eumastigonodesmus* (p. 211)

Family HAPLODESMIDAE

Although *Prosopodesmus* has the appearance of a pyrgodesmid, its gonopods are much more polydesmid-like. Hoffman (1979) created a new subfamily within the Haplodesmidae to receive *Prosopodesmus*. The Haplodesmidae belong to the same suborder as the Polydesmidae, but they occupy a different superfamily. the TRICHOPOLYDESMOIDEA.

The single representative of this family in Britain, *Prosopodesmus panporus*, undoubtedly an introduction, is now well established in hothouses of the Royal Botanic Gardens at Kew. It has not yet been found in its natural tropical home.

Prosopodesmus panporus Blower & Rundle
(Fig. 60)

Prosopodesmus panporus Blower & Rundle, 1980: *Myriapodologica* 1(4): 27–34, Figs. 1–3, 6–8

Male	19	Length: 3.3–3.8 mm	Breadth: 0.45–0.50 mm
Female	20	3.8–4.3	0.50–0.51

Almost without pigment, white to cream white. Head almost hidden by a large collum tergite. Second tergite much broader with paranota forwardly directed embracing head and collum. Second tergite broader than all succeeding tergites which are strongly arched, their mid-lateral paranotal edges incized into three lobes, each tergite with three transverse rows of domed tubercles. An outermost pair of tubercles carries the ozopores; these are present on all diplopodous rings, from the fifth, to the seventeenth in the male and the eighteenth in the female. This complete series of ozopores is unique within the order Polydesmida (hence the trivial name).

This is one of the smallest diplopods; it is shorter than *Macrosternodesmus palicola* (p. 212) but slightly broader. *Adenomeris gibbosa* (p. 62) and *Stygioglomeris crinata* (p. 60) are even shorter but are twice the breadth.

Distribution

British Isles: Known only from hothouses of the Royal Botanic Gardens, Kew where it was first discovered by Dr. A. J. Rundle in March 1975. The species is well established in several houses; Dr. Rundle has collected mating pairs and all stadia from the Palm House in 1976.

The one other species of the genus, *P. jacobsoni* occurs pantropically and has been introduced into Brazil (São Paulo and Rio de Janeiro) and the United States (Florida). The species is thought to have originated in the Oriental region and to have been introduced into the western hemisphere. It is not known to which country *P. panporus* is indigenous.

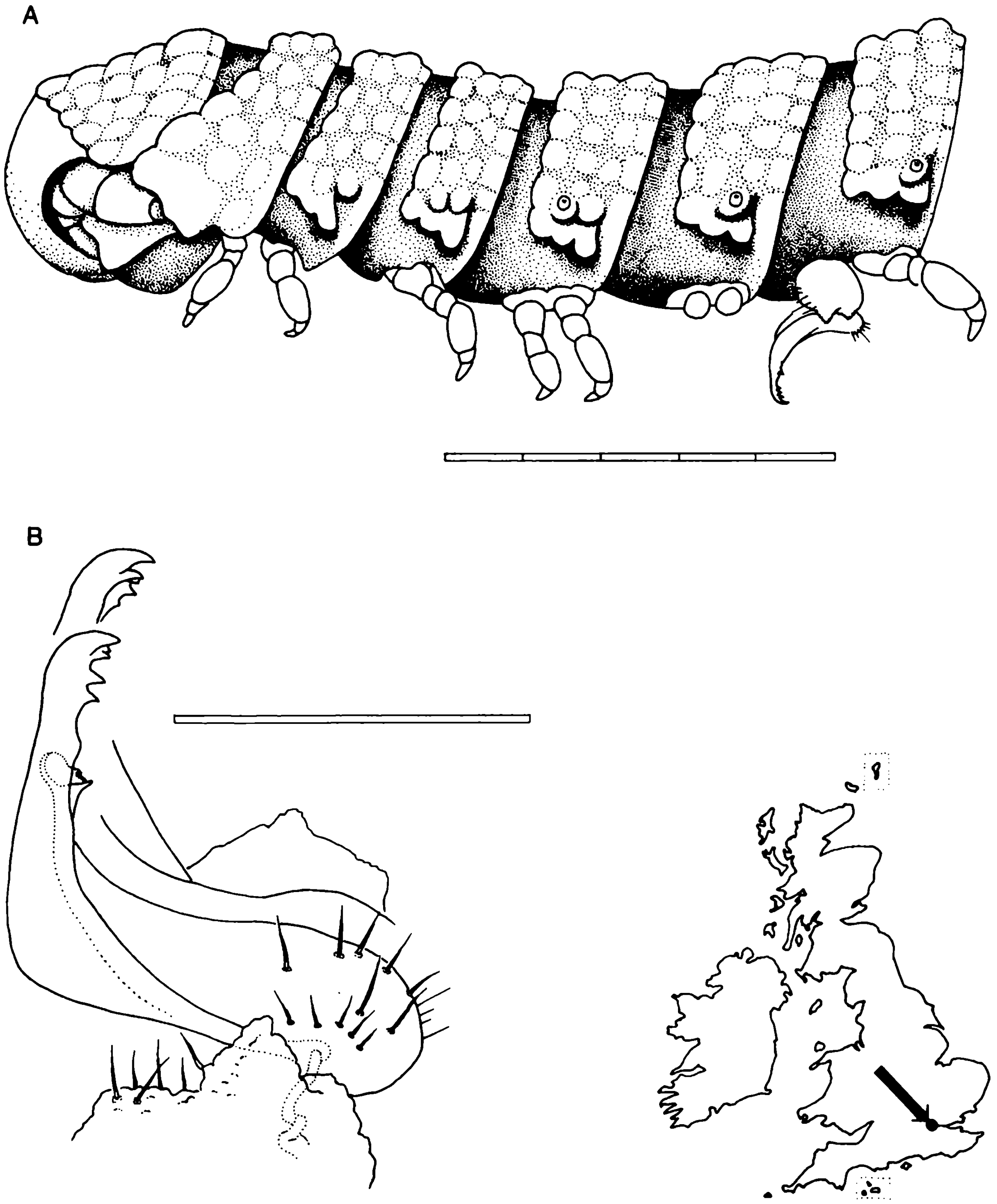


Fig. 60. *Prosopodesmus panporus.* A. The head and rings I to VII of the male; note the laterally expanded paranota of ring II which embrace the collum; B. Gonopods viewed from the right and slightly ventrally.

Family POLYDESMIDAE

The members of this family in Britain are easily recognized by their flat backs and characteristic pattern of sculpture between the paranota. *Eumastigonodesmus boncii* is an exception with a smooth dorsal surface and is included in this family on the basis of its gonopod anatomy; it is one of the smallest species; it is included in the key to Macrosternodesmidae for convenience only.

Polydesmid gonopods often possess a small chamber at the apex of the seminal or prostatic groove and a group of setae at the exit. Invariably the gonopod aperture is cordate with an anterior projection from the posterior margin providing a transverse shelf supporting the coxae. The coxae are hollowed out on their ventral sides to receive the telopodites and are in contact with each other in the mid-line.

Key to the species of Polydesmidae

This key refers specifically to adults and is merely a guide; safe diagnosis ultimately depends on comparison of the gonopods and epigynes with the figures (Fig. 61). Gonopods may be viewed *in situ* by removing some of the legs anterior to the gonopods on one side, but it may be found necessary to detach the gonopod.

1. Narrower, usually less than 1.5 mm broad. All tubercles well raised and distinct **2**

Wider, usually broader than 1.5 mm. Tubercles *either* moderately raised in larger species, 15–25 × 2.0–3.7 mm *or* poorly raised in medium species, 10–18 × 1.5–2.5 mm **3**

2. 10 mm long or less, 0.1–1.0 mm broad. Adults with 19 rings (maturity is indicated by gonopods of male or epigynal flanges of female) (Fig. 67) .... *Brachydesmus superus* (p. 206)

10–16 mm long, 1.2–1.6 mm broad. Adults with 20 rings (Figs. 61B, H; 64) .... *Polydesmus inconstans* (p. 200)

3. Medium size, but less than 18 × 2.5 mm; tubercles low **4**

Large size, greater than 15 × 2.0 mm; tubercles moderately well raised **5**

4. 10–17 mm long, 1.5–2.5 mm broad. Tubercles low. First rectilinear tergite anterior to V. Common species (Figs. 61C, I; 66) .... *Polydesmus denticulatus* (p. 204)

13–18 mm long, 1.6–2.3 mm broad. Tubercles very low. First rectilinear tergite posterior to V. Rare species in south east (Figs. 61A, G; 63) .... *Polydesmus testaceus* (p. 198)

5. First rectilinear tergite usually posterior to the seventh. Lighter in colour, slightly yellowish. Common in the southern half of Britain and all Ireland. (Figs. 61E, K; 65) .... *Polydesmus gallicus* (p. 202)

First rectilinear tergite usually the seventh or anterior to the seventh. Darker, brown – light brown. Common everywhere (Figs. 61, D, F, L, J; 62) .... *Polydesmus angustus* (p. 194)

Polydesmus angustus Latzel
(Fig. 62)

Polydesmus complanatus var *angustus* Latzel, 1884: *Bull. Soc. Amis Natur. Rouen* (1883) (2), *19*: 267

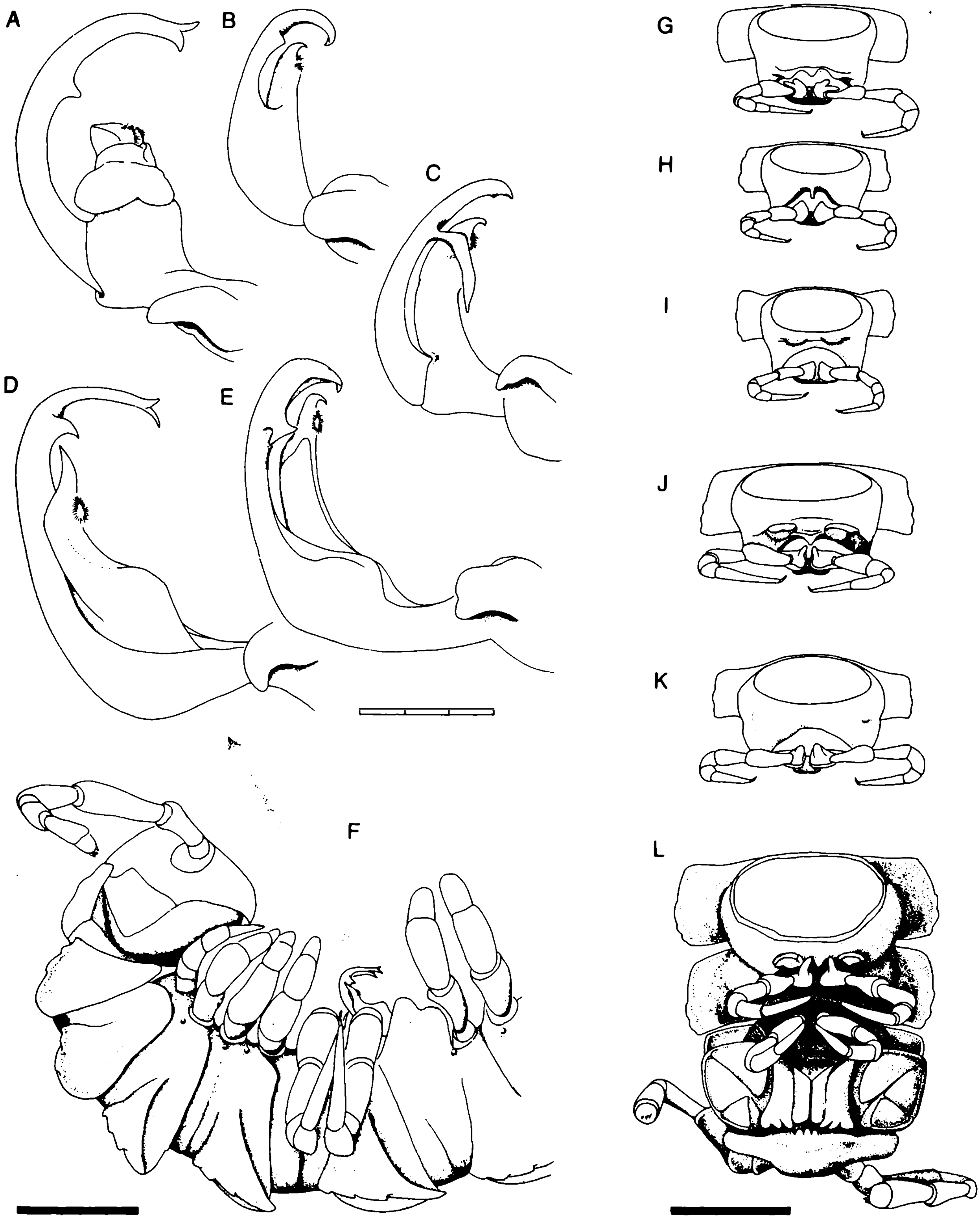
Male	Length: (13) 16–21 (28) mm	Breadth: 2.0–3.0 (3.4) mm
Female	15–19 (22)	2.3–3.0 (3.7)

The male has much more robust legs than the female and usually appears to be much the larger of a pair. This is the largest and most common species of the genus in Britain; it is the most frequently recorded millipede in England and Wales and the third most frequent in the British Isles. Medium to moderately dark brown; sculpture moderately clear; boss well raised but transverse division only discernible in the female; first and second rows of tubercles indistinct. Dorsal setation very fine and hardly noticeable.

Biology. There is no field data on life cycle, principally due to the difficulty of referring sub-adult stadia to species with certainty. Verhoeff (1928) reared a close relative, *P. complanatus*, a similar sized eastern European counterpart of *P. angustus*, from eggs of one generation to adult females of the next which themselves laid eggs. This was the first time a millipede had been reared through its entire life history. Verhoeff records a period of 22 months from eggs hatching to egg laying in the next generation. Since his animals were kept in a heated room he supposed the cycle would extend over 2.5–3 years in the field.

Adults are relatively fleet; Manton (1954) records a speed of 22 mm per second by adult *P. angustus* of equivalent size to our fastest julid, *Tachypodoiulus niger* (p. 135) which walked at 13 mm per second. Adult *Polydesmus* spp appear to range over wide distances; Pearson & White (1964) found *P. angustus* and *denticulatus* in pitfalls on rather unpromising upland grassland in Snowdonia. By contrast, the sub-adult stadia are usually highly aggregated.

Fig. 61. Gonopods and epigynes of *Polydesmus*. The isolated telopodites of the gonopods are on the left and the epigynal regions of ring III and the second pair of legs of the female on the right. A, G. *Polydesmus testaceus*; B, H. *P. inconstans*; C, I. *P. denticulatus*; D, J, *P. angustus*; E, K, *P. gallicus*; F, *Polydesmus angustus*, lateral view of male with legs 6 and 7 displaced to reveal the gonopods; simplified version of Fig. 62C: L, Ventral view of the head and rings I–III in a female.


A
B
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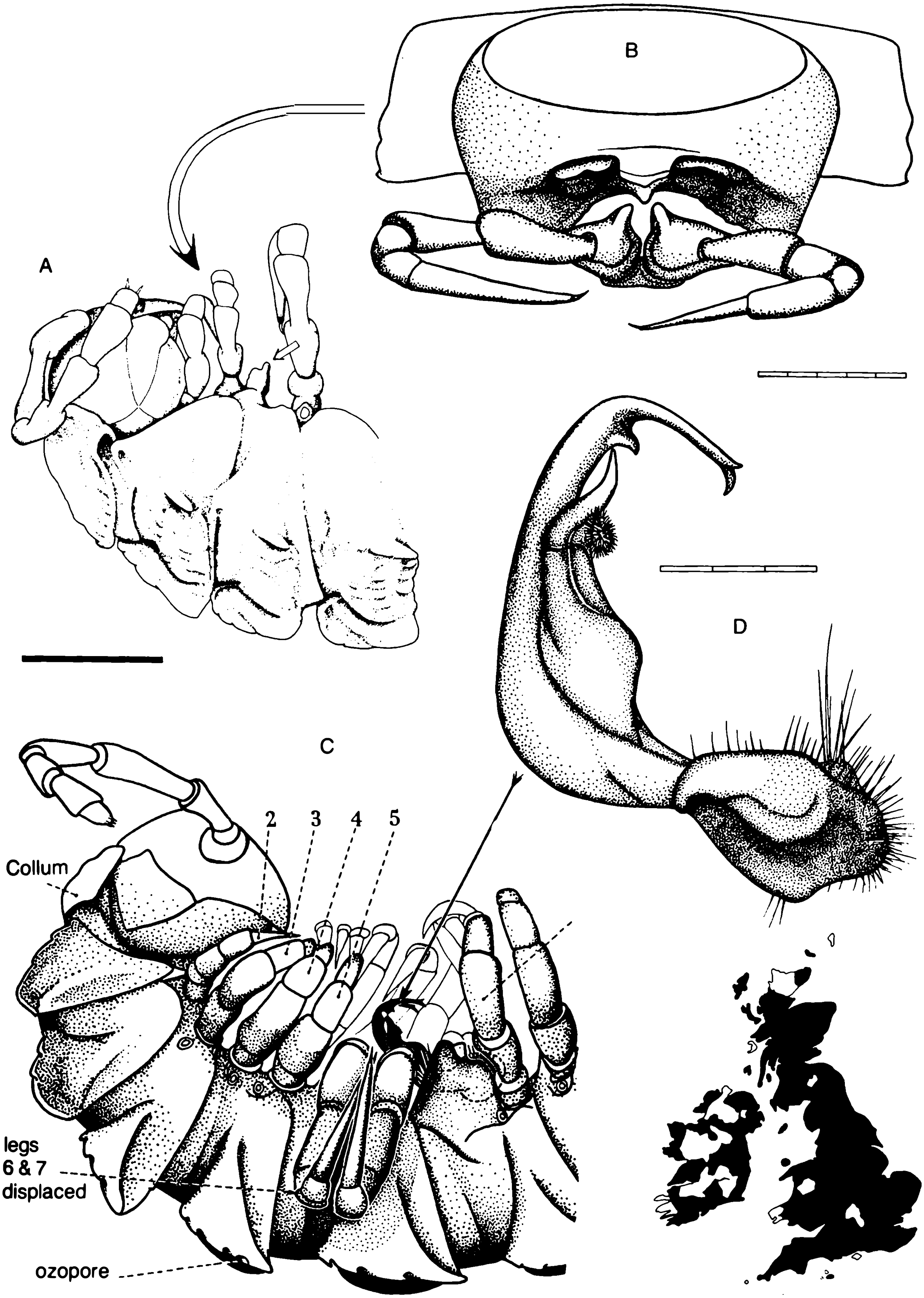
Distribution

British Isles: It would seem to be merely a matter of time before the few blank vice-counties on the map are filled in. *P. angustus* is probably the most eurytopic of our species, extending more often than any other into the most acid situations such as pine woods and heaths and yet being present practically everywhere that millipedes occur. In woods it is often associated with *P. denticulatus* (p. 204), but unlike this latter, *P. angustus* is also common around farmland, in gardens and wasteland. Sometimes it occurs in large numbers under seed boxes, pieces of wood, old sacking and other impedimenta around cultivated land and is often implicated in damage to strawberries, lupin roots and other garden produce.

Europe: Confined to the west, France, N.W. Switzerland, Holland, Belgium, Norway, W. Germany. Further east and south replaced by *P. complanatus* (= *P. complanatus illyricus* Verhoeff).

Introduced into N. America, Mexico.

Fig. 62. *Polydesmus angustus.* A. Head and rings I–III of a female in dorsolateral view to show epigynal flange (open arrow) in profile; B. Ring III and second pair of legs in anteroventral view to show epigyne and modified coxae (see Fig. 61L). C. Lateral view of the head and rings I to VIII of the male; legs 6 and 7 have been displaced to show the gonopods; the first pair of legs lies mesial to the second and cannot be seen; D. Isolated telopodite of the right gonopod enlarged.


B
A
D
C
2
3
4
5
Collum
legs
6 & 7
displaced
ozopore

Polydesmus testaceus C. L. Koch
(Fig. 63)

Polydesmus testaceus C. L. Koch, 1847: *System. der Myriapoden, 135*

Male	Length: (13) 14.0–17.5 (18) mm	Breadth: 1.5–2.0 (2.3) mm
Female	(13) 14.5–18.0	1.5–2.0 (2.3)

Measures are from Rolfe (1935) with those of Schubart (1934) in brackets where they exceed British dimensions; specimens from northern France are larger still (20 × 3.0 – 3.3).

Light brown to light reddish brown. All tubercles indistinct; first and second rows just discernible; lateral edges of paranota very indistinctly toothed, almost smooth. First field row not developed, second and third very weakly. First rectilinear tergite (7) 8.

Distribution

British Isles: First recorded by Pocock (1903) from Walton on the Naze, Essex (VC19), secondly from east Kent (VC15) under stones in a chalk pit at Wye and from allotments in Folkstone (Rolfe, 1935). Rolfe describes the species and figures the gonopods and the vulvae; he comments that the animal is more active than *P. angustus* (p. 194) and *P. inconstans* (p. 200). More recently found by Turk (1944) under stones at Reskandinnick, near Cambourne, Cornwall (VC1, females only) and at Polbathic, near St. Germans in east Cornwall (VC2). Both Cornish localities were areas of accumulation of wind blown sand of high calcium carbonate content. The species has been recorded from a cave in Surrey (VC17) by Hazelton & Glennie (1962) and in 1978 a quarry in North Kent (VC16) by Davis (1978).

Europe: Only from France, Germany, west Switzerland (Rhone valley and Geneva), Belgium and Holland. As in Britain, the European occurrences have always been from chalk or limestone habitats, under stones in quarries, etc.

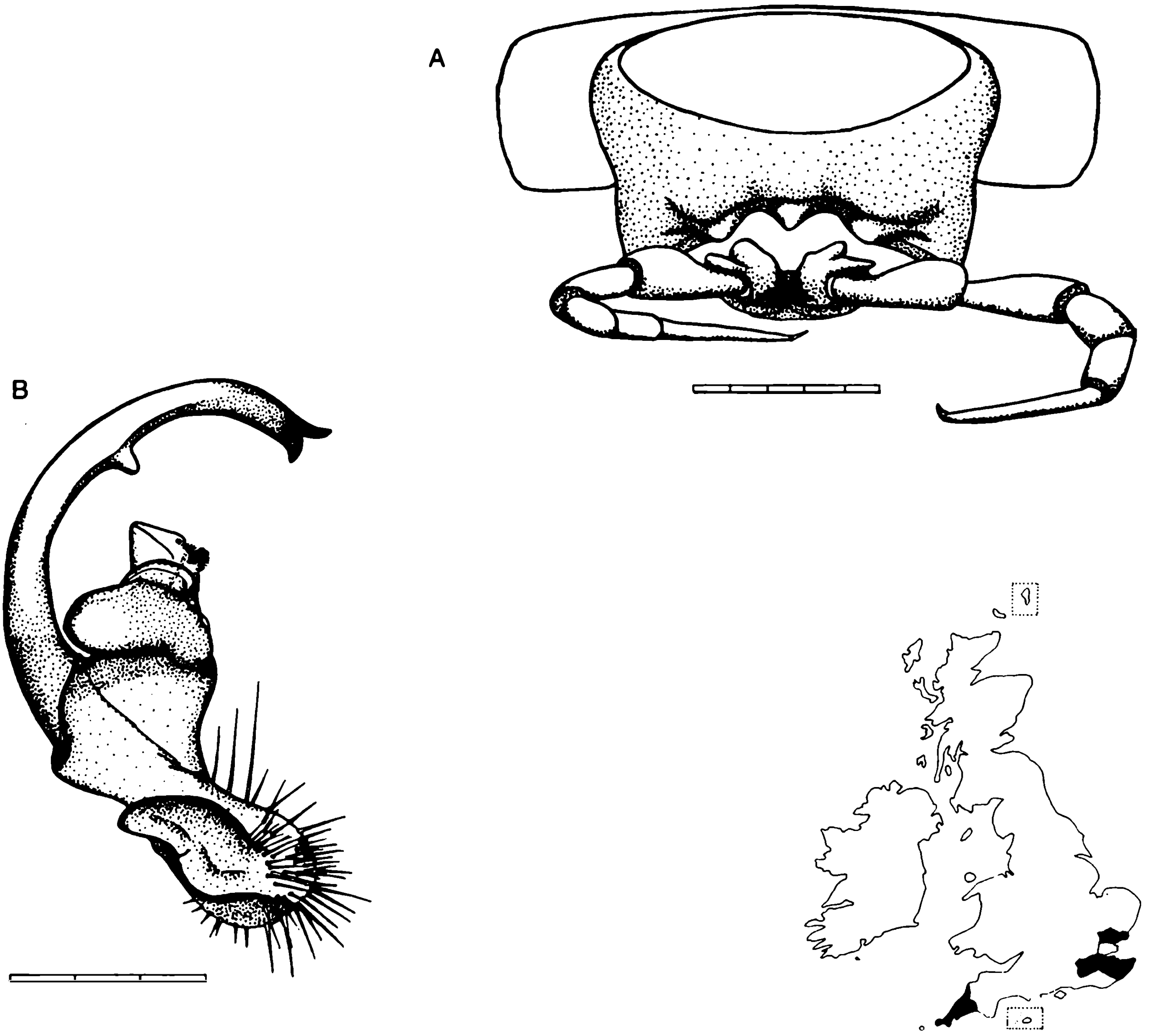


Fig. 63. *Polydesmus testaceus*. A. Ring III showing epigyne behind the second pair of legs (see Fig. 61L for orientation); B. Isolated telopodite of right gonopod in external profile.

Polydesmus inconstans Latzel
(Fig. 64)

Polydesmus inconstans Latzel, 1884: *Bull. Soc. Amis. Sc. Nat. Rouen,*
19: 269, pl. 1, Fig. 3
P. coriaceus of Blower (1958) and European authors but not of Porat, 1870
Palmen (1949) first recognized that the Central and Northern European animals referred by authors to *P. coriaceus* Porat should rightly belong to Latzel's *P. inconstans*. See also Schubart (1957) and Demange (1970).

Adult Length: 10–16 mm Breadth: 1.2–1.6 mm

A small brown to dark brown species characterized by the clarity and prominence of the dorsal sculpture. All tubercles clear and well raised; boss distinctly divided transversely; teeth on edge of paranota not very obvious; first rectilinear tergite (6) 7.

Biology. Snider (1981a, b, c) has described the life cycle from field and laboratory observations. In a maple wood in Michigan, USA, females oviposit from late May to mid-August. They probably make six or seven successive nests (up to 22 separate ovipositions were secured in the laboratory) giving a mean total of 500 eggs. These develop to stadia VI and VII by autumn and mature and reproduce the following spring. Death follows the ovipositing period. Field temperatures ranged from 15–23°C from late spring to autumn. In Britain, temperatures would probably be too low and of too short duration to allow this annual cycle.

Distribution

British Isles: First recorded by Pocock (1906a) from Somerset and referred by him to Latzel's *P. inconstans.* Usually found in ones and twos but sometimes in larger numbers in association with cultivation. Often recorded from the nests of moles. It is the fourteenth most frequently recorded millipede in Britain (cf. *P. denticulatus*, 15th). Recently, in a paper on the fauna of limestone quarries in Kent, Lincolnshire and Derbyshire, Davis (1978) found *P. inconstans* the most abundant millipede, more abundant than the two schizophyllines.

Europe: France, Switzerland, Germany, Norway, Sweden and Denmark. West Poland, Austria, Czechoslovakia. Synanthropic in S. Finland, Estonia and Russia.

Introduced into USA, Canada and Iceland.

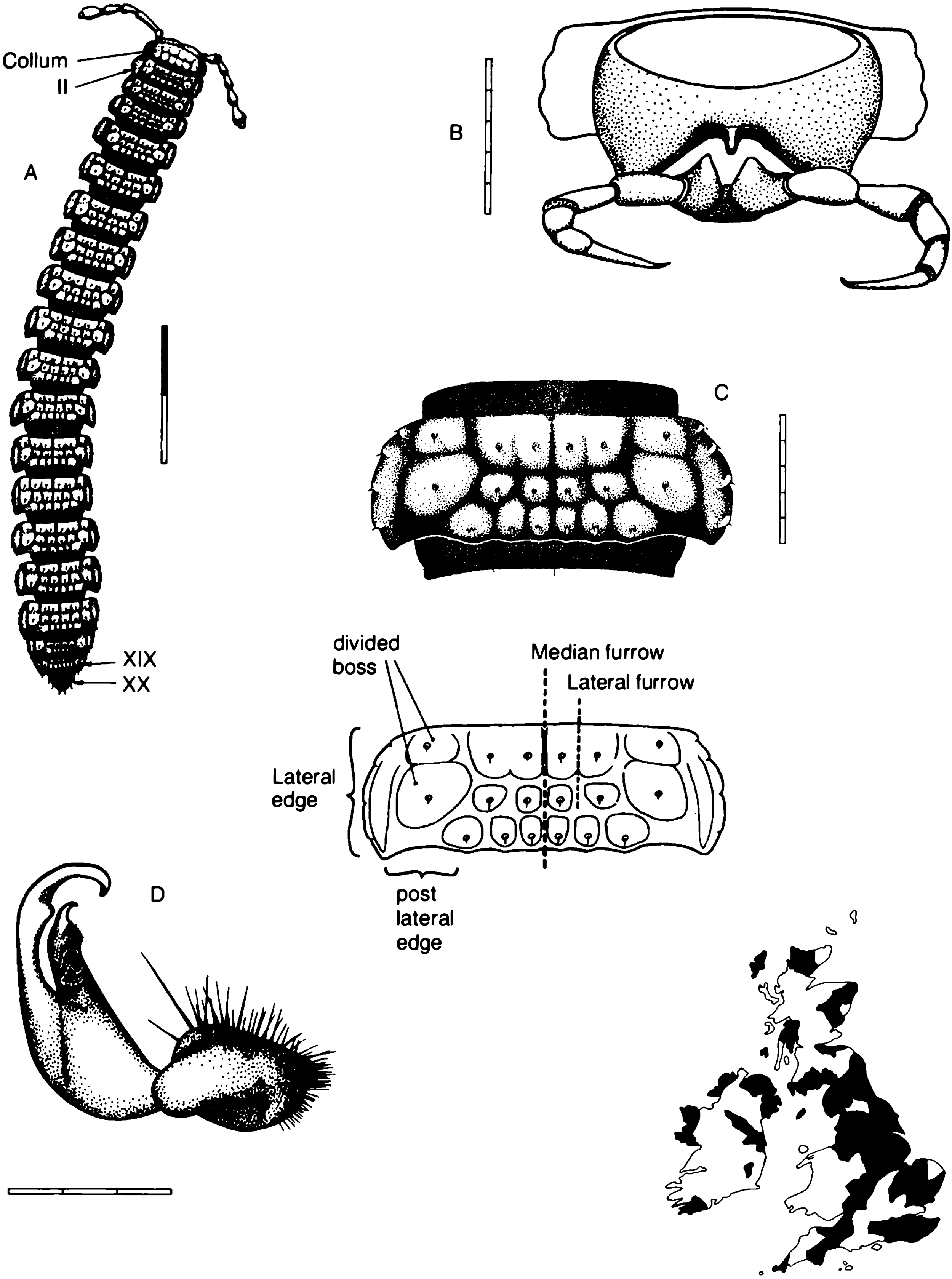


Fig. 64. *Polydesmus inconstans.* A. Dorsal view of a female to show sculpture, legs omitted; B. Ring III showing epigyne behind the second pair of legs (see Fig. 61L for orientation); C. Enlarged view of ring IX; outline to illustrate nomenclature beneath; D. Isolated telopodite of right gonopod in external profile.

Polydesmus gallicus Latzel
(Fig. 65)

Polydesmus gallicus Latzel, 1884: *Bull. Soc. Amis Sci. Natur. Rouen 1883* (2) *19*: 269

P. gallicus subspecies *typica* Brolemann, 1910: *Bull. Soc. d'Hist. nat. Toulouse 43*: 61, Figs. 1–17

P. coriaeceus Porat, 1870 (see *Note*)

Adult Length: 15–20 mm Breadth: (2.0) 2.2–2.8 mm

Brolemann had material of this species from Ireland and commented on their narrowness compared with French and English examples (2.0–2.2 mm). One of our largest species, slightly smaller than *P. angustus* (p. 194) and more greyish dusky brown in colour, often with a yellowish straw tinge. Boss high and clear but not obviously divided; first and second row of tubercles with distinct secondary furrows; first rectilinear tergite (7, 8) 9.

Brolemann describes three subspecies from the south of France; the British examples agree with the typical form in possessing a tooth on the internal edge of the secondary ramus opposite to the external rectangular lobe (Fig. 65C). Turk (1947) thought that the sculpture of a female from a cave in Somerset resembled that of the subspecies *reflexa* but its size and the epigynal region of the third segment conformed to the variety *tolosana* of the typical form. Demange (1970), in the same paper in which he refers the *P. coriaceus* of European authors to *P. inconstans*, points out that *P. gallicus* is a synonym of *P. coriaceus* Porat, in particular Brolemann's sub-species *atlantica*. I have thought it better at the moment to be content with removing *coriaceus* from the British list before reoccupying it with another well-known British species.

Distribution

British Isles: First recorded by Pocock (1893) from Ireland. The most northerly record in Britain is from south west Yorkshire (63) but it occurs further north in Ireland where it is the eighth most commonly recorded species of millipede compared with eighteenth in England. Kime (1978) has the species eighth in his list of Surrey records but he says it is much commoner in the west and there is only a single record from Kent. Records come from woodland and open country often in very damp situations, swampy regions, ditches etc.

Europe: France: Normandy, Charente; in the Pyrenees two subspecies occur in addition to the typical form found in Britain.

Introduced into USA.

Note: The sub-species *P. gallicus atlantica*, the true synonym of *P. coriaceus* Porat occurs in Madeira, the Azores and Spain. Strictly speaking, the typical form of *P. gallicus* Latzel, which occurs in Britain, should be named *P. coriaceus gallicus*.

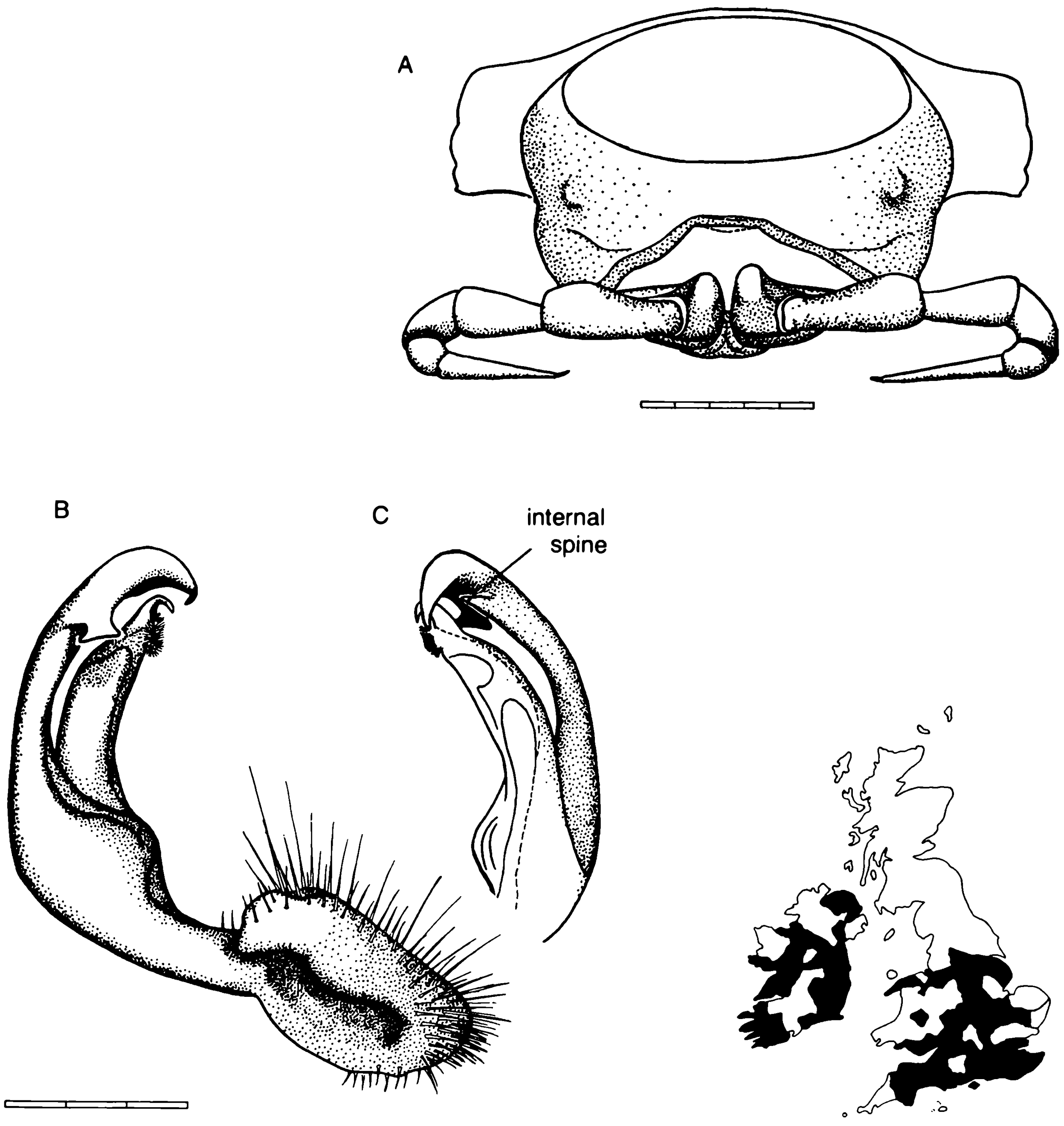


Fig. 65. *Polydesmus gallicus*. A. Ring III showing epigyne behind the second pair of legs (see Fig. 61L for orientation); B. Isolated telopodite of right gonopod in external profile; C. Inner profile of apex of telopodite of right gonopod to show internal spine.

Polydesmus denticulatus C. L. Koch
(Fig. 66)

Polydesmus denticulatus C. L. Koch, 1847: *System. der Myriapoden: 135*

Adult Length: 10–17 mm Breadth: 1.5–2.5 mm

Light brown to darker reddish brown. Sculpture only moderately clear, first row of tubercles not distinct, second and third rows more distinct but all tubercles low. First rectilinear tergite (2) (3) 4, placed more anteriorly than in all other species. Teeth on lateral edge of paranota distinct; setation more evident than in *P. angustus* but less distinct than in *Brachydesmus superus*; setae slightly expanded distally, almost clavate. The long external lateral process of the secondary ramus is most distinctive and can be seen by careful observation *in situ* but sometimes this process is lost during pairing.

Biology. Data on this species from field samples suffer from an admixture of *P. angustus* and there is no certain way of distinguishing the young stadia of these two species. However, in a Cheshire wood the majority of the individuals in the samples were believed to belong to *denticulatus*; stadium II appeared in large numbers in early July. By autumn there were equal numbers of stadia II to IV and twice as many stadium V. This stadial spectrum reappeared in the spring following. Numbers of stadia VI, VII and VIII were always very low. Adults trapped on the site showed peak activity in June and July; males were in excess and 10 to 30% of these had lost the lateral processes of the secondary rami. As in other species of *Polydesmus* nests are constructed against some hard substrate. Mr. Eales found many nests built upon the concave inner side of beech nuts measuring 5 mm diameter and 2 mm high.

Distribution

British Isles: First recorded by Pocock (1901) from Carlisle in Cumbria. A common inhabitant of old oak and mixed deciduous woods, sometimes quite acid; often found in association with *P. angustus* but not often recorded away from woodland as is *angustus* and not encountered in the large aggregates formed by the young stadia of *angustus*. It is ranked the fifteenth commonest millipede (cf. *inconstans* 14th, *gallicus* 15th, *angustus* 3rd) although it should possibly come higher in the list, as its present position probably results from confusion with *angustus*. Probably commoner in the west; Bagnall, on recording its presence in Durham, referred to it as 'quite a rare animal'.

Europe: Widely, as far east as the Urals, south east to Romania, Bulgaria and south to Northern Italy and Yugoslavia. In Germany Schubart (1934) says it is seldom found in woods, more often in farmland, gardens, etc. which is the very antithesis of its distribution in Britain.

Introduced into Newfoundland.

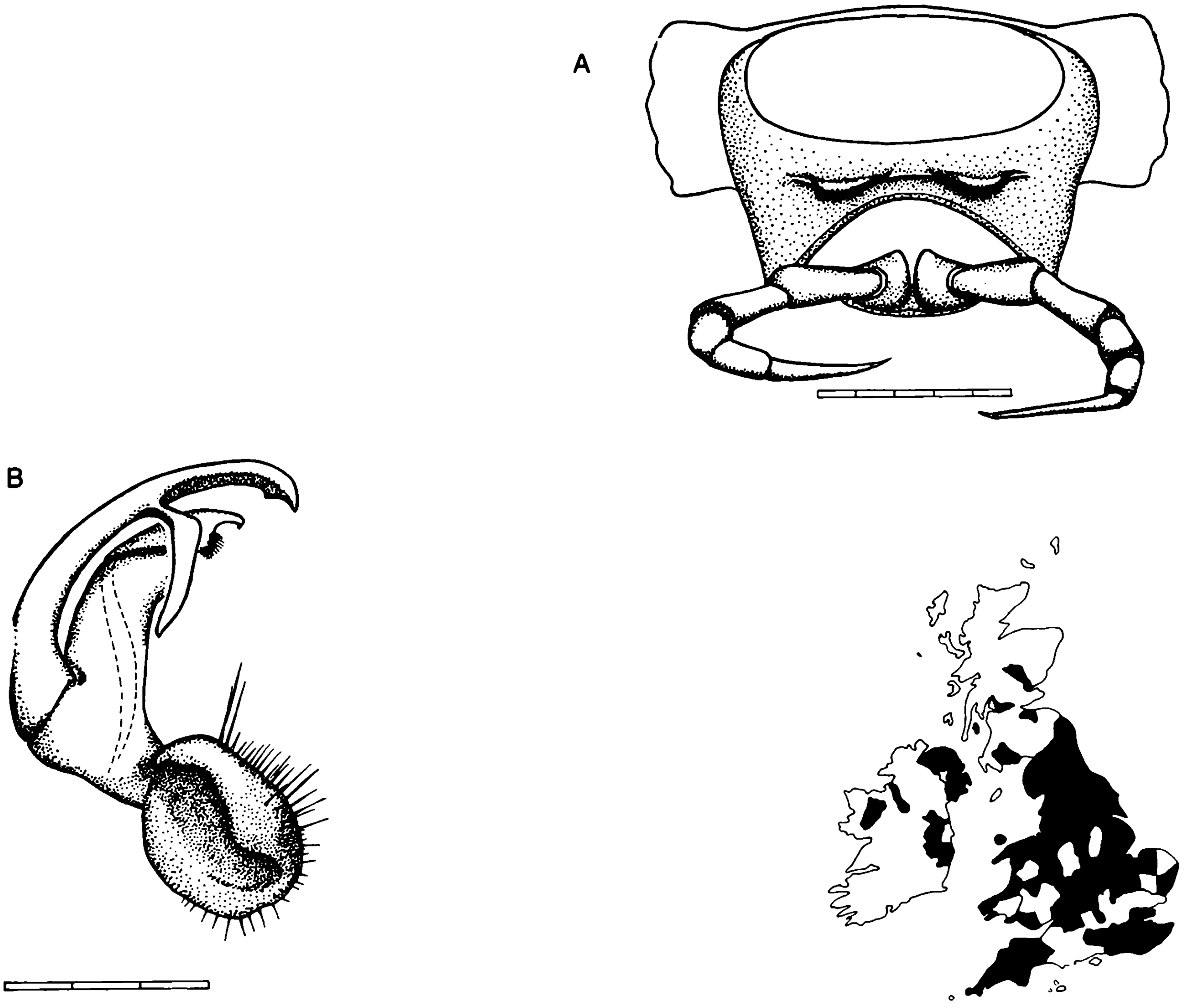


Fig. 66. *Polydesmus denticulatus*. A. Ring III showing epigyne behind the second pair of legs (see Fig. 61L for orientation); B. Isolated telopodite of right gonopod in external profile.

Brachydesmus superus Latzel
(Fig. 67)

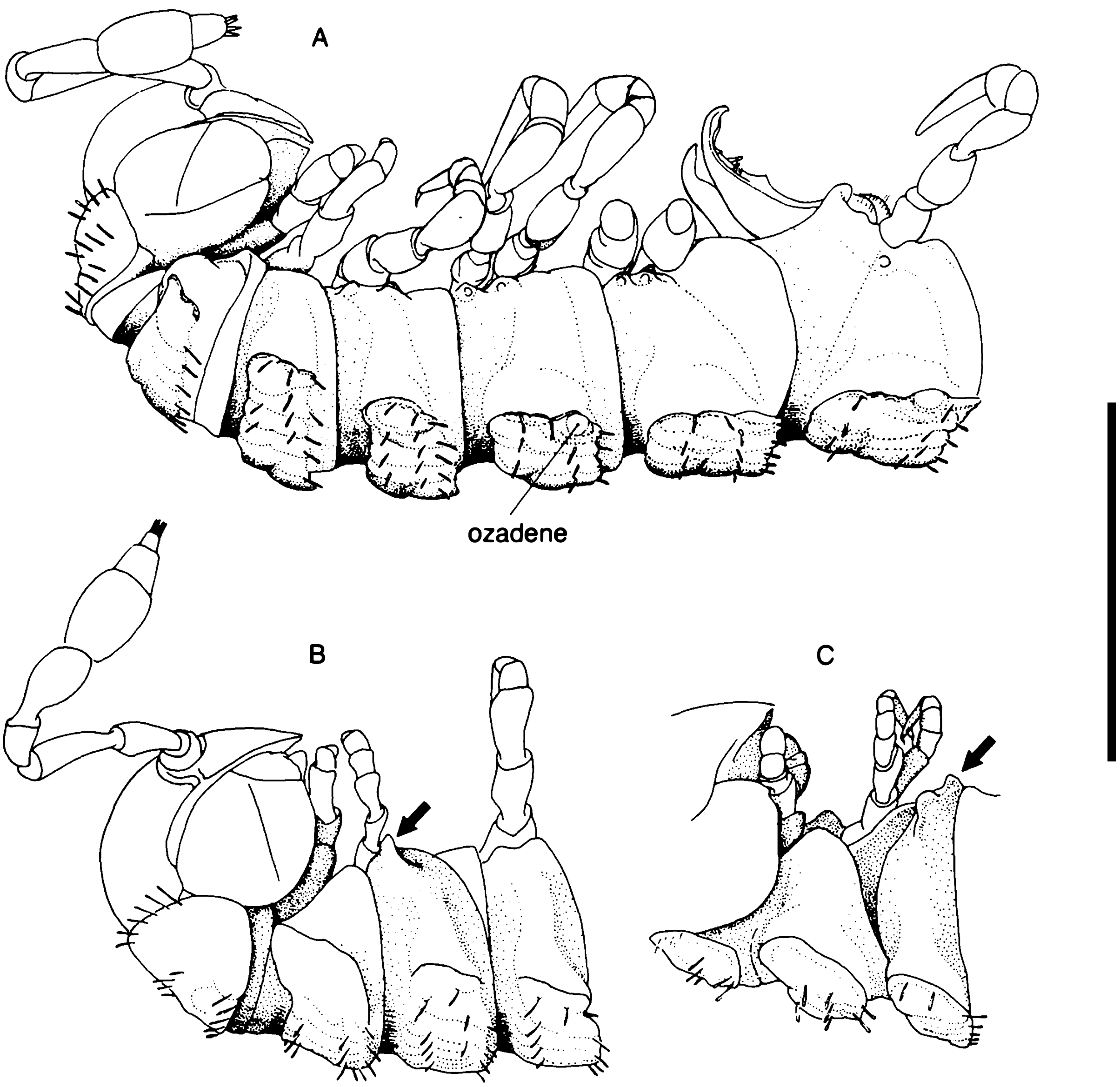
Brachydesmus superus Latzel, 1884: *Die Myr. ost.-ung. Mon.*, *2*: 130–132, p. 16, Fig. 69

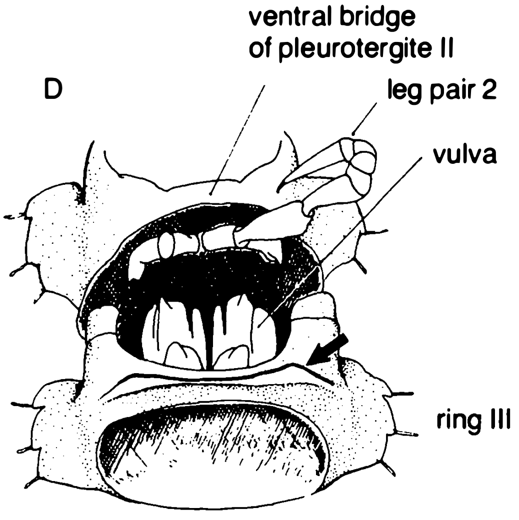
Adult Length: 8.0–10.0 mm Breadth: 0.8–1.1 mm

Sometimes almost white, sometimes slightly greyish to light brown; overall colour impression in life partly dependent on the colour of the gut contents transmitted through the transparent cuticle. Dorsal sculpture fairly distinct as in *Polydesmus inconstans* (p. 200) but sometimes less distinct. The gonopods are not so evident as in *Polydesmus* spp., they lie closely against the ventral surface between the preceding pairs of legs. Care must be exercised to ascertain the presence of the epigynal ridge of the adult female with nineteen rings before rejecting an individual as a sub-adult of *Polydesmus* sp.

Biology. Stephenson (1961) reared this species from eggs to adults and gives interesting biological details. Eggs were laid in elaborate nests similar to those constructed by *Polydesmus* spp., about 50 per nest; these hatched in his laboratory within a month to six weeks and developed through to stadium VII in 5–6 months (maximum 9 months). Since most development in the field occurs in the summer months, the course of development in the field was found to be similar to that in the laboratory. Females died after laying eggs but two females constructed two nests with 20–30 eggs in each; forty females made only one nest. No adult females were taken in the field between August and October. Blower (1979) also gave evidence that this is an annual species. In a south Wales oak wood, early instars appeared in the samples by July, most of which had proceeded to stadium III by late autumn. In the following spring stadia V and VI had appeared suggesting some development over winter. Very few adults overwintered on the Welsh site. Stephenson describes an interesting adaptation for overwintering of the males; some of these reach stadium VII with their full complement of segments but with only rudiments of the gonopods. A further moult ensued the following spring with the appearance of functional gonopods but without the addition of new

Fig. 67. *Brachydesmus superus*. A. Head and rings I–VII of a male in lateral view. The openings of the tracheae are visible on rings V and VI immediately dorsal to the coxae of the legs. The ozadenes can be seen near to the posterior edges of the paranotal keels of rings V and VII. The telopodites of legs 6 and 7 have been removed; these would normally obscure the gonopods which lie mesial to them – usually closer to the trunk than in this figured specimen; B. Head and rings I to IV of a female in lateral view; C. Head and rings I to III of a female, slightly more ventro-lateral than in B; D. Ventral view of rings II and III eased slightly apart, of the same female as in B and C. The epigynal flanges are indicated by bold arrows in B, C and D; these, or the vulvae if exposed, are the only evidence that the animal with nineteen rings (telson included) is an adult of *Brachydesmus superus* and not a sub-adult of *Polydesmus* spp.


A
ozadene
B
C


ventral bridge
of pleurotergite II
D
leg pair 2
vulva
ring III

additional segments. Lewis (1972) suggested that a similar epimorphic moult may occur in overwintering females but would be morphologically unrecognizable. Stephenson gives dimensions of all larval stadia and the logarithms of these plotted against stadia extrapolate readily to the lowest adult length but not the upper. The hidden epimorphic moult may account for the rather wide range in adult length; it would be interesting to discover if the spring adults were bimodal in size.

Distribution

British Isles: First recorded by Pocock (1893) from Ireland and since in most of the counties of Britain and many in Ireland; it is the seventh most frequently recorded species of millipede. Very numerous in limestone woodland and limestone districts generally but also widespread in cultivated loams; it is commonly found in arable fields and gardens associated with *Blaniulus guttulatus* (p. 116) fairly deep in the soil. Found fairly frequently in caves where there is an area of damp clay-loam, also in the nests of moles.

Europe: Recorded throughout most of Europe; many subspecies have been described by Verhoeff, especially from the Mediterranean region.

Introduced into the USA, Madeira, Azores, Canaries and Cape Verde Island.

Family MACROSTERNODESMIDAE

The two smallest polydesmidans included here still present problems of classification. Schubart (1934) had them in the family Strongylosomidae, now called Paradoxosomatidae; Demange (1981) includes *Macrosternodesmus* in the Leptodesmidae, and *Ophiodesmus* is included in the Polydesmidae. They are included in this family Macrosternodesmidae by Hoffman (1979) and it is this classification which is adopted here. In the present uncertainty there is little point in giving a definition of the family over and above that implicit in the inclusion of these two species.

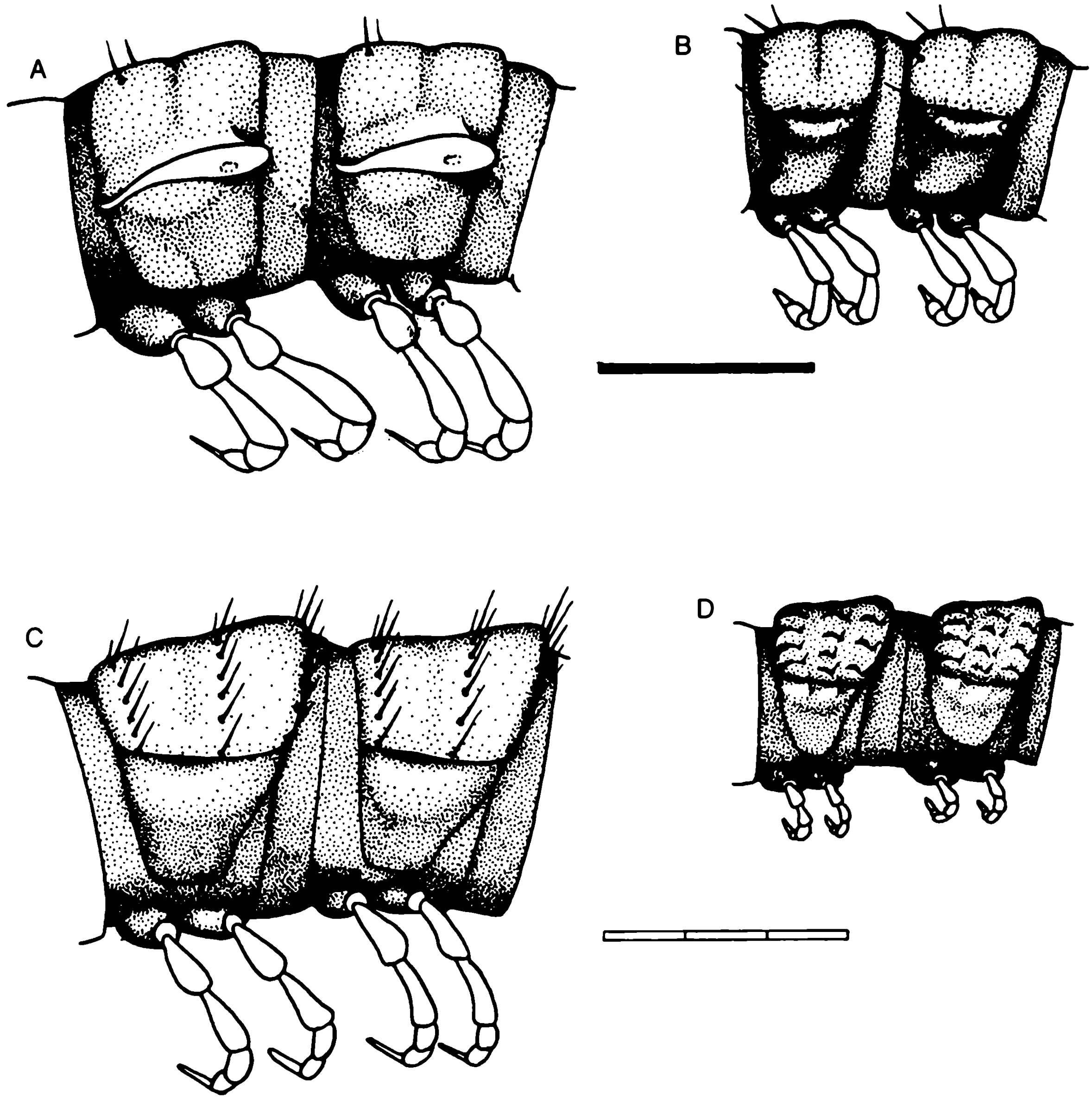


Fig. 68. Paradoxosomatidae (A, B) and Macrosternodesmidae (C, D). Lateral views of rings XII and XIII: A. *Oxidus gracilis*; B. *Stosatea italica*; C. *Ophiodesmus albonanus*; D. *Macrosternodesmus palicola*.

Key to the species of Macrosternodesmidae and Eumastigonodesmus

In the following key *Eumastigonodesmus* has been included for ease of discrimination although it is a member of the family Polydesmidae.

1. Metazonites with smooth dorsal surface and lateral edges **2**

Metazonites with tuberculate dorsal surface and toothed lateral edges. Adults with 19 rings; 0.3–0.4 mm broad, 3.5–4.0 mm long; three transverse rows of very short setae. (Figs. 68D, 70) .... *Macrosternodesmus palicola* (p. 212)

2. Three transverse rows of distinct setae. Adults with 20 rings; 0.5–0.8 mm broad, 5.0 mm long. (Figs. 68C, 71) .... *Ophiodesmus albonanus* (p. 214)

Three transverse rows of very short setae. Adults with 19 rings; 0.3–0.4 mm broad, 4.5 mm long. (Fig. 69) .... *Eumastigonodesmus boncii* (p. 211)

Eumastigonodesmus boncii (Brolemann)
(Fig. 69)

Fig. 69. *Eumastigonodesmus boncii.* External profile of left gonopod. The flagellum and its sheath have been partly uncoiled from their normal state: 'coiled like a gimlet'. Redrawn and enlarged from Brolemann's figure in his original description (Brolemann, 1908).

Mastigonodesmus boncii Brolemann, 1908: *Bull. Soc. ent. France, 1908* (9) 171–173

Male and female with 19 tergites, telson included   Length: 4.0–4.5 mm

Completely without pigment. Tergites arched with three transverse rows of very short setae like *Macrosternodesmus palicola* (p. 212), but much smoother dorsally and with lateral edges of the paranota smooth and not toothed as in *M. palicola.* Gonopods short and stocky with the seminal groove separated from the main ramus in a pseudoflagellum. Much shorter than the biramous gonopods of *M. palicola*.

Distribution

British Isles: Recorded on one occasion only by Bagnall (1922) from Gibside, County Durham, associated with *Macrosternodesmus palicola*.

Europe: Known only from France: Pyrénées-Atlantique, Haute-Garonne and Ariège in the months of November and December (Demange, 1981).

Macrosternodesmus palicola Brolemann
(Fig. 68D, 70)

Macrosternodesmus palicola Brolemann, 1908: *Bull. Soc. Ent. France, 1908:* 94–96, Figs. 1 & 2

Titanosoma jurassicum Verhoeff, 1910 (see Verhoeff, 1911)

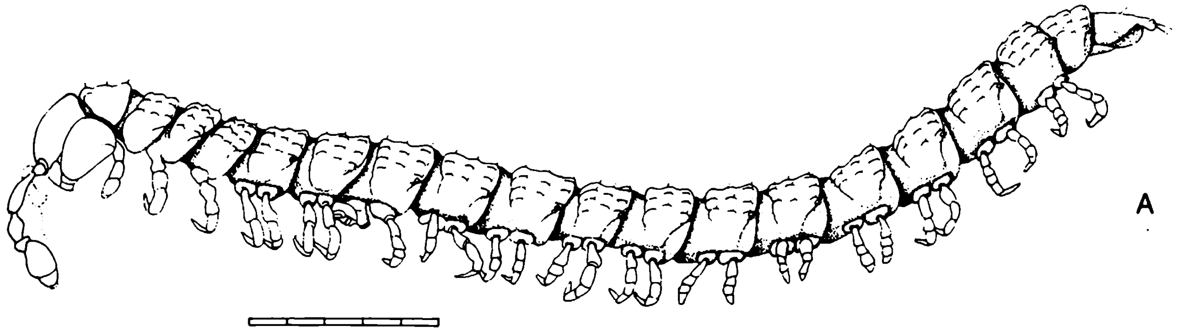
Adult Length: 3.5–4.0 mm Breadth: 0.3–0.4 mm

Almost without pigment, the dark gut contents apparent through the cuticle. Tergites tuberculate, their lateral edges with three teeth. Setae very short and not immediately apparent. This is the smallest diplopod, belying the name which Verhoeff applied, no doubt with a touch of humour; *Prosopodesmus* is about the same length but fractionally broader; *Ophiodesmus albonanus* is slightly longer but nearly twice as broad. Both sexes with 19 rings in the adult.

Distribution

British Isles: This is another small pale species first recorded by Bagnall (1912A), from Northumberland. By 1921 Messrs Bagnall, Jackson and Brade-Birks had added eight more vice-county records from their homes and habitual hunting grounds in the northeast and northwest. Further records were not to hand until Messrs Kime & Barber added eight more county records from the south in the 1960s and 1970s. Dr. Eason found it in Gloucestershire and Dr. Lewis from Hereford at the second field meeting of the British Myriapod Group. More recently Dr. Rundle (*in litt.* 1.6.79) produced the species from eighteen sites in nine 10 Km squares in Bedfordshire – a record bout of recording! The species is often found along with *Ophiodesmus albonanus*. Kime (1978) thinks the species may be quite common in suitable calcareous localities; he has found it in shallow rendzina soils at ten different sites in England, and on *no other soil*; seven of his finds were from beechwoods growing on chalk and all were in the first four months of the year.

Europe: Here too the species is clearly a collector's item. It was first found by Brolemann at his home in Pau, next by Verhoeff near his home in Bavaria, then by Schubart from his home in Potsdam. Enghoff also records it from his garden and elsewhere in Denmark. Lohmander records it from several sites in Sweden, whilst Demange (1981) now records it from the Pyrénées-Atlantique, Haute-Garonne, Lot-et-Garonne, Tarn and Tarn-et-Garonne.



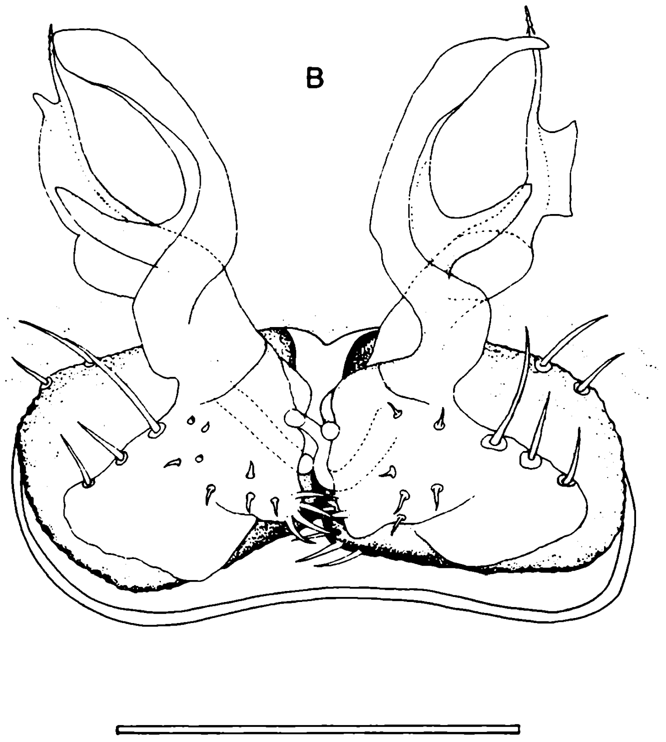


Fig. 70. *Macrosternodesmus palicola*. A. Lateral view of male; the ozadenes can be seen at the posterior corners of paranota V, VII, IX, X, XII, XIII and XV to XVII; B. Ventral view of gonopods seated within the gonopodial aperture on ring VII.

Ophiodesmus albonanus (Latzel)
(Fig. 68C, 71)

Paradesmus albonanus Latzel, 1985: *Mit. Naturhist. Mus. Hamburg, 12*: 107

Adult Length: 4.5–5.0 mm Breadth: 0.5–0.8 mm

Almost without pigment. Tergites smooth, without tubercles, with smooth lateral edges to the paranota. Three transverse rows of moderately long setae, much more evident than those of *Macrosternodesmus palicola* (p. 212). Both sexes with 20 rings in the adult.

Distribution

British Isles: First recorded by Bagnall (1918) from Bath in Somerset and Swanage in Dorset. Seven more English vice-counties were added by Bagnall and Brade-Birks and a record from Edinburgh by Bagnall in 1925. Further records were not made until the sixties and seventies; ten more vice-county records were made, mainly by Kime, but also by Eason, Blower and Barber. The most recent finds have been in Monmouth, Cheshire, Northwest Yorkshire and Bedford in which county Dr. Rundle has twelve records in seven 10 Km squares.

Europe: Very few records from France (Aisne, Alpes de Haute Provence, Haute Garonne and Seine), Germany, Denmark, Holland and Sweden.

Also reported from Newfoundland.

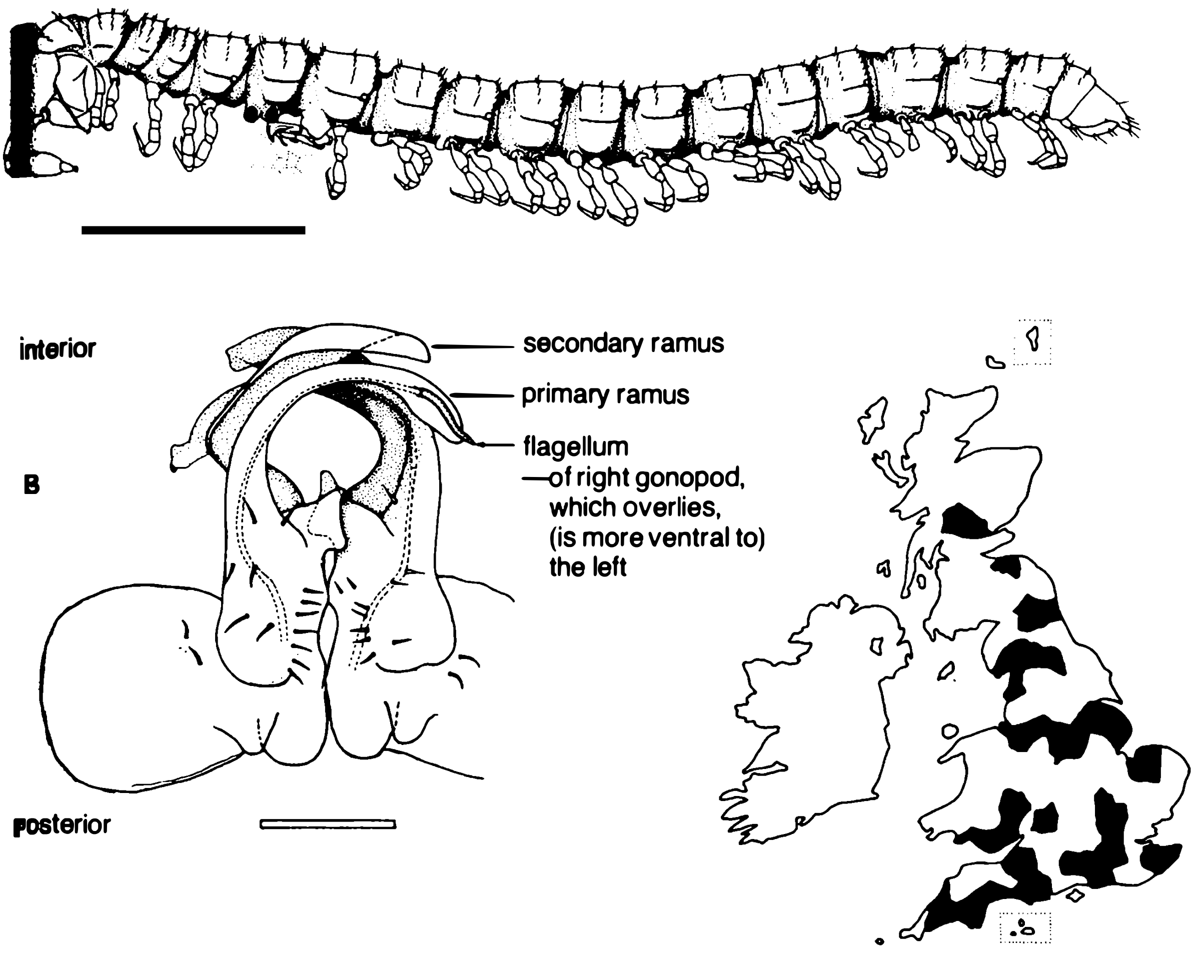


Fig. 71. *Ophiodesmus albonanus*. A. Lateral view of male; legs 6 and 7 on ring VI have been removed to reveal the gonopods which lie mesial to them. The ozadenes can be seen at the posterior corners of paranota V, VII, IX, X, XII, XIII and XV to XVIII; B. Gonopods in ventral view; the right telopodite overlaps (is more ventral to) the left.

Family PARADOXOSOMATIDAE

This family is probably the most homogeneous and well-worked group within the Polydesmida. It is characterized by the dumb-bell shaped gonopod aperture in which the coxae are wholly separated from each other. Most of the paradoxosomatids have simple smoothly arched backs. The group includes many large tropical species; our two representatives are both introductions from warmer climes, *Oxidus gracilis* is confined to hothouses or greenhouses; *Stosatea italica* occurs in the open in Kent, but its natural home is around the Mediterranean.

Key to the species of Paradoxosomatidae

1. Metazonites often without setae; dorsally rich chestnut brown colour with edges of paranota contrasting amber colour. Paranotal keels very distinct, with flanged edges. Adults over 2.0 mm broad, 16–23 mm long. (Figs. 68A, 72) .... *Oxidus gracilis* (p. 218)

Metazonites with setae along anterior edge, paranotal keels not so distinct. Yellowish – brown colour. Adults smaller, 1.2–1.5 mm broad, 11–14 mm long (Figs. 68B, 73) .... *Stosatea italica* (p. 220)

Oxidus gracilis (C. L. Koch)
(Fig. 68A, 72)

Fontaria gracilis C. L. Koch, 1847: *System. der Myriapoden, 40*: 142
Paradesmus gracilis and *Orthomorpha gracilis* of authors

Male	Length: 16–21 mm	Breadth: 2.0–2.3 mm
Female	17–23	2.0–2.5

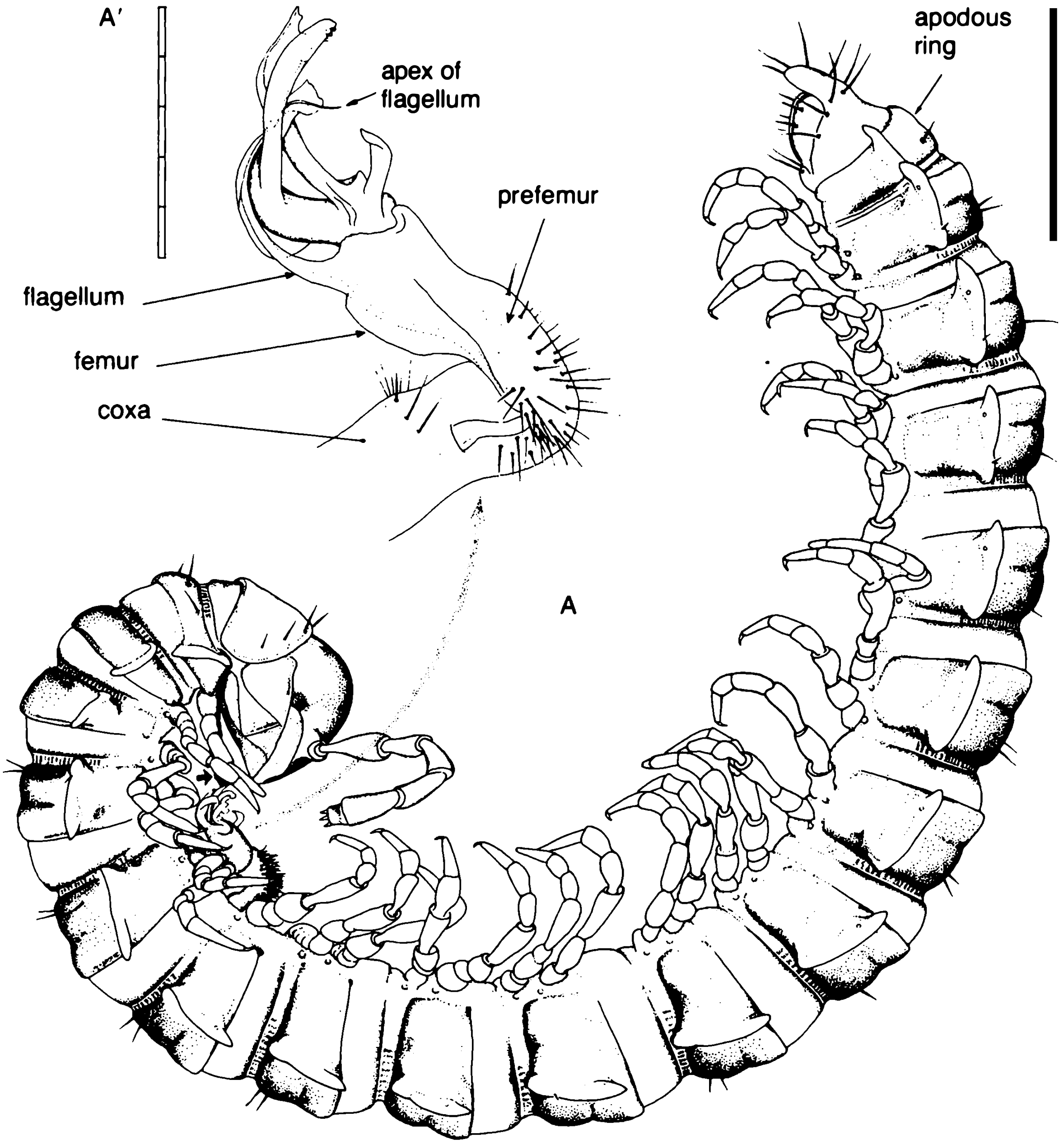
A very characteristic animal with polished chestnut to dark reddish, black-brown dorsum, very prominent keel like paranota, prozonites ventral surface, caudal projection and limbs, a contrasting light amber colour. Immature stadia light amber to cream. Setae on the metazonites often absent.

Biology. The life-history of this cosmopolitan hothouse species has been described by Causey (1943) and Lang (1959). According to Causey, clutches of 40–150 eggs are laid in all months of the year; no elaborate nest is constructed. At 22°C hatching occurs in 9–10 days and the mature Stadia VIII are achieved in 5 to 6 months. The economic significance of the species is discussed by Brade-Birks (1930) and Rolfe (1937); some aspects of its behaviour are described by Cloudsley-Thompson (1951).

Distribution
British Isles: First recorded from Edinburgh in 1898 (Evans, 1900) and from Kew Gardens in London (Pocock, 1902). There followed about a dozen records of its occurrence in hothouses, nursery gardens and botanic gardens scattered throughout Britain previous to the 1939 war but only six records since, from Berkshire, Somerset and Yorkshire. Dr. Rundle has recently sent me living material from Kew Gardens. The most recent records are from Lanarkshire (VC 77), Yorkshire (VC's 64, 65), Derbyshire (VC 57) and two Irish counties.

Europe and beyond: The species was probably indigenous in East Asia, but is now free-living throughout the tropics, especially maritime regions including the West Indies and many islands in the Atlantic and Pacific. It extends into temperate North and South America, all of Europe (first recorded from Holland in 1882) and Japan where it lives in hothouses, gardens and adjacent compost heaps but is not able to overwinter in the absence of some source of warmth.

Fig. 72. *Oxidus gracilis*. A. Lateral view of male; the first pair of legs is hidden mesial to the second pair (black arrow); frequently most of the setae on the anterior part of the metazonites are missing; the small seta placed anteriorly on the lateral keel are difficult to see and are often missing; on this individual, only the setae on keels V and X were visible; A′. Enlarged view of the inner profile of the right gonopod; B. Ventral view of ring VII to show gonopods with the apical processes of the right overlapping (ventral to) those of the left.


A′
apex of flagellum
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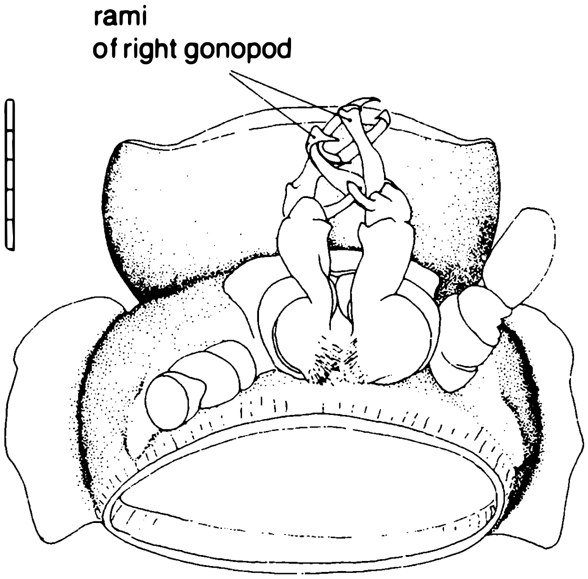
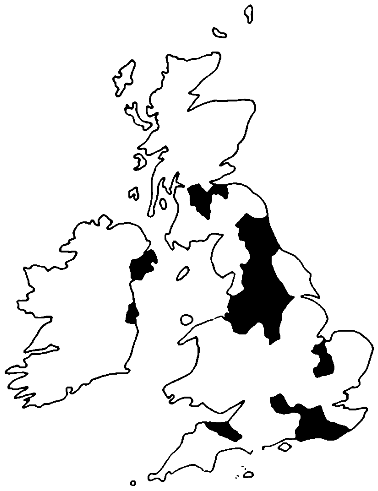
apodous ring
A


rami of right gonopod



Stosatea italica (Latzel)
(Fig. 68B, 73)

Strongylosoma italicum Latzel, 1886: *Bull. Soc. Entom. Italiana, 18*: 309
Entothalassinum italicum (Latzel) of First Edition.

Adult Length: 11–14 mm Breadth: 1.2–1.5 mm

Rich chestnut brown to light brown or even pale cream, evenly distributed; immature stadia fawn to pale cream. Setae along the anterior edge of the otherwise smooth metazonites. Paranota less developed than in *Oxidus gracilis*.

Distribution

British Isles: First recorded from East Kent (VC 15) in the Vicarage garden at Wye and also by the roadside near Cold Harbour farm in decaying vegetation (Brade-Birks, 1922) and later from Westwell, near Ashford by Sankey (1955, *pers. com.*). Recently from Surrey (Kime, 1968) from the grounds of Guildford Grammar School (coll. A. W. Taylor) and in litter in an old chalk quarry nearby (coll. Barber); later from North Essex (VC 19) in Saffron Walden, near a hospital under an old sack and a fallen log (Barber, 1969) and from Monmouth (VC 35).

Kime (1978) referring to the Guildford records in 1967, says that the species has not been seen in Surrey since this date. He observes that all sites were calcareous and/or near to habitation.

Europe: This species is distributed around the Mediterranean: Italy, Yugoslavia, Corsica, Sicily, Sardinia, Elba, Tunisia, Monaco and the Croatian coast but it has occurred far from its normal range in France, Switzerland, Holland, Belgium, Luxembourg and the Atlantic island of Madeira.

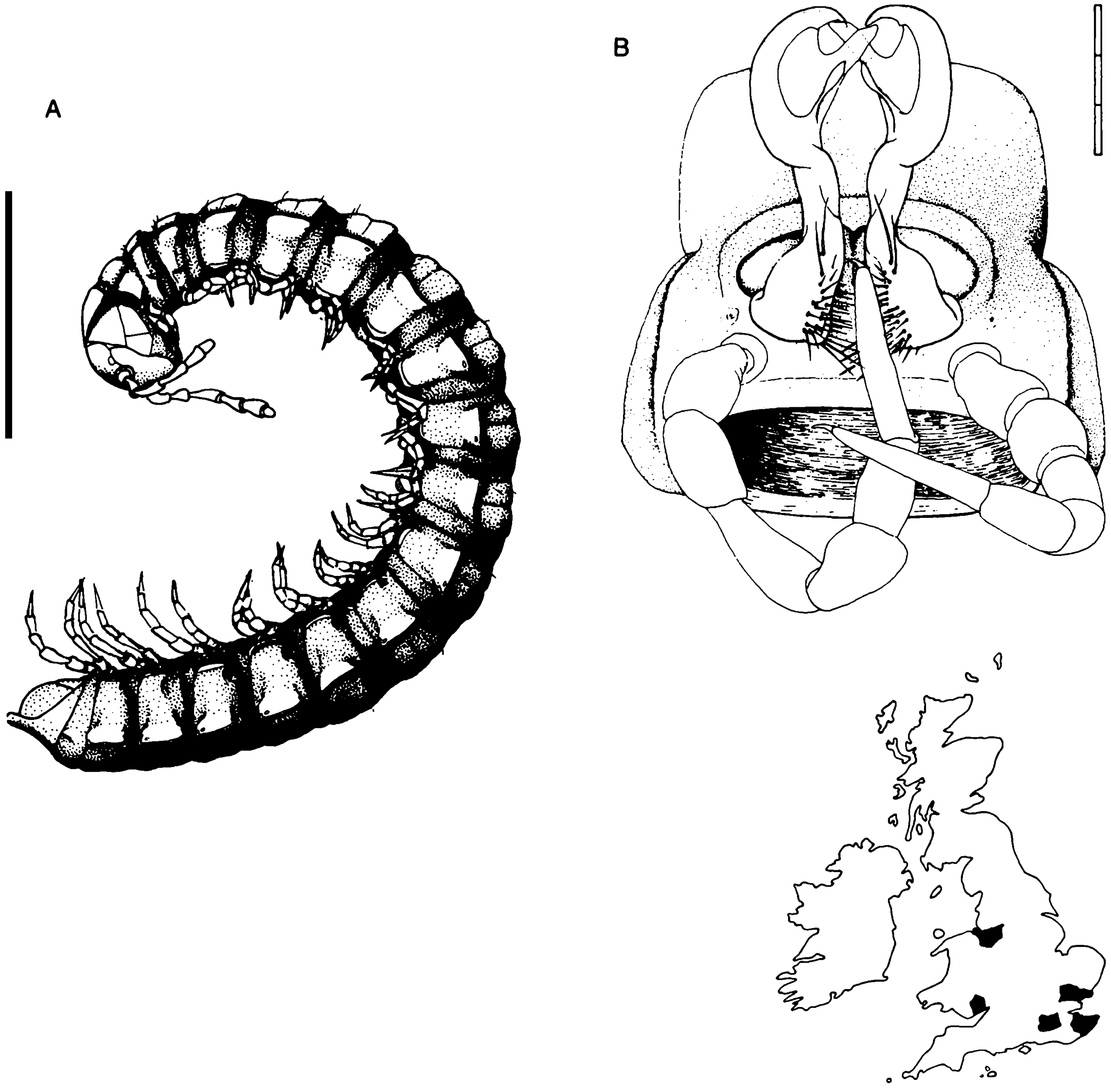


Fig. 73. *Stosatea italica*. A. Lateral view of a female; B. Ventral view of ring VII with gonopods and leg-pair 9.

Acknowledgements

For early encouragement and example I am indebted to Professors Graham Cannon, Ralph Dennell and Percy Butler, and Drs. Brade-Birks and Owen Gilbert. For a long period I was fortunate to have had much valued material help and support from, and discussions with, Dr. Sidnie Manton. My continued interest and enthusiasm has been maintained by the fresh minds of Drs. Charles Brookes, A. M. Kheirallah, Colin Fairhurst, John Round, Peter Miller, Nabil Kayed, Allan Davidson, Henk Littlewood and Miss Helen Read, who have worked with me, and by my past and present esteemed colleagues on the teaching staff at Manchester.

Members of the British Myriapod Group have been a tower of strength. Dr. Eason has favoured me with his support and much material help; amongst younger colleagues, I have valued most the interest and help I have had from Mr. Desmond Kime and Mr. Tony Barber who, apart from doing much to advance the study of Myriapoda themselves, have advanced my own comprehension of many finer details and supplied me with material from their collecting. Dr. Adrian Rundle must rival Richard Bagnall in his ability to find new and rare animals and he has shared all his finds with me. Mr. Declan Doogue fills the Rundle niche in Ireland and has likewise shared with me the fruits of his field work. The least experienced but most enthusiastic help has come from several generations of undergraduates; not being able to mention all by name, I only hope they received as much intellectual encouragement in return.

Dr. Henrik Enghoff was kind enough to read through my typescript with meticulous care, correct many errors of fact and procedure, discuss matters of opinion and add much detail on extra-British distribution. Professors Richard Hoffman and François Sahli also read the typescript and suggested many stylistic and factual corrections. Like all myriapodologists I owe much of my knowledge of the literature and many contacts with colleagues throughout the world, to Messieurs J.-M. Demange and J.-P. Mauriès of the Centre International de Myriapodologie in the Paris Museum. Dr. D. M. Kermack has set a high standard and has gently encouraged me in my attempts to achieve it.

To all these ladies and gentlemen I owe a debt of gratitude which I gladly record here.

Glossary

aestivation A summer period of inactivity, usually in response to dry conditions.

aliform Shaped like a wing.

ambulatory Applied to legs: walking legs, not modified for some other purpose such as gonopods.

anal scale (or **sub-anal scale**) The ventral sclerite terminating the trunk, immediately under the anal valves; sometimes elongated as in *Enantiulus armatus.*

anal valves The terminal pair of lateral sclerites placed either side of the anus.

anamorphosis Post-embryonic development in which the number of segments increases at each moult. *Cf.* **epimorphosis, hemianamorphosis.**

antennomere An individual part, 'segment' or 'joint' of the antenna. Millipede antennae have eight antennomeres.

apodeme An intucked part of the cuticle, serving as an attachment for muscles (e.g. the tracheal pouch) or to provide a blind ending pouch (e.g. the apodematic tube and ampullae in the vulva which serve as spermathecae).

apodous Without legs.

aposematic Warning coloration: bright or contrasting colour patterns associated with distastefulness (*n.* aposemosis).

base-rich soil Rich in exchangeable bases, or cations of basic salts, especially calcium. A soil may be base-rich and still show a concentration of hydrogen ions on the acid side of neutrality.

biramous Applied to legs with two branches, inner endopodite and outer expodite, as in Crustacea; in contrast to uniramous, the condition in insects and myriapods.

brachit Anterior flange of the solenomerite (the tubular part of the posterior gonopod or opisthomerite) in julids.

bursa The main body of the vulva of the female within which lies the spermatheca or seminal vesicle, to the anterior of which is applied the operculum.

cardo The proximal coxomere or part of the mandible, visible externally as one of the two cheek lobes (*pl.* **cardines**).

cheirite *lit.* 'hand'; the hand-like lobe which is the telopodite of the gonopod in Craspedosomatidae.

chilognath *lit.* lip-jawed; referring to the fusion of the second pair of jaws, the first maxillae, into a lower lip or gnathochilarium. Applied to all diplopods except Pselaphognatha. (In centipedes it is the first trunk limbs which form a lower lip, hence Chilopoda.)

collum The tergite of the first trunk segment.

congeneric Belonging to the same genus.

copulatory Stage of a male with full equipment for sperm transfer; to distinguish from a resting, intercalary male in which the gonopods and other secondary sexual characters are regressed.

coxal sacs Extrusible thin walled sacs in the coxae of the legs.

coxomere Part of the mandible.

crypsis Camouflage; colouration to blend with the background.

deferent canals The ducts carrying sperm from the testis to the genital opening.

detritivore Consumer of detritus, usually implying dead vegetation; almost synonymous with **saprophage.**

dignathous With two pairs of jaws, mandibles and first maxillae.

diplopodous ring A trunk unit with two pairs of developed limbs; (units V to the last podous).

diplosegment A unit of the trunk in which at least the tergite and lateral pleurites serve two pairs of legs or rudiments of same.

dorsum The dorsal surface.

epigeic Living on or above the surface of the soil.

epigyne *lit.* outside the genital opening; the anterior part of the ventral pleural bridge of ring III in polydemid females.

epimorphosis Post-embryonic development in which the number of segments does not increase at each moult. *Cf.* **anamorphosis, hemianamorphosis.**

eurytopic *lit.* widely placed; extending over a wide range of habitats *cf.* **stenotopic.**

eversible vesicle A thin-walled sac which can be turned inside out (see **coxal sac**).

extrinsic Refers to muscles which originate distal to the organ to which they are attached; specifically referring to coxal retractors attached to the tracheal pouch apodeme.

flagellum A whip-like structure arising from the promerite of julid gonopods or from the peltogonopod of a nemasomatid.

flagellum groove A groove within the solenomerite of julid gonopods housing the flagellum.

frontal setae A pair of setae either side of the median line of the frontal surface of the head; absent in Cylindroiulini.

fungistasis Suppression of fungal growth.

glabrous Smooth, without setae.

gnathal lobe The most distal of the three parts of the three-jointed mandible; not visible laterally as are the two proximal parts, the cheek lobes, cardo and stipes.

gnathochilarium *lit.* jaw-lip; the lower lip formed mainly from the fused first maxillae (analogous to the labium of insects which is formed by the fusion of the second maxillae).

gonopods The modified legs of ring VII in the male (sometimes also rings VI and VIII), used for transferring sperm to the female.

gonopods proper The structures actually used to transfer the sperm to the female, as distinct from **paragonopods** or **peltogonopods** which play a subsidiary role in insemination.

gonopodal sac The sac within which the gonopods of julids are retracted; they are extended by eversion of this sac.

gula The sternite of the collum segment which forms the posterior part of the gnathochilarium; also called **hypostoma.**

gynandromorph Individual with some characters of both male and female.

halophile *lit.* salt-loving; showing a preference for coastal habitats (perhaps due to the influence of salt spray). *cf.* **littoral.**

hemianamorphosis Post-embryonic development which is initially anamorphic (more segments added at each moult), and later epimorphic (without increase in segments at each moult).

hypostoma see **gula.**

insemination The introduction of sperm into the female where it is stored until used to fertilize the eggs.

intercalary A stage in the development of males in which gonopods and other secondary sexual structures regress; ideally intercalated between two **copulatory** stages.

intromittent *lit.* inside putting; descriptive of the organ which is inserted into the female genital opening to transfer sperm.

iteroparous Repeated egg laying; used particularly to indicate laying eggs in more than one breeding season (*n.* **iteroparity**).

juliform having the appearance of a cylindrical trunk with fused tergites, pleurites and sternites as in the Julida (and exotic orders Spirobolida and Spirostreptida).

littoral Living between tidemarks on the sea shore *cf.* **halophile.**

litter A collective term including all the dead vegetation which dies back or falls on to the surface of the soil; woodland litter is mainly composed of dead leaves or needles, but also twigs, fruits, bud scales etc.

maculate Spotted.

mandibles The first pair of jaws comprising three parts, the cardines and stipes laterally (the cheeks or jowls), and terminal mesial gnathal lobes which bear the chewing processes.

maxillae The second pair of jaws, fused together in the mid-line to form the lower lip or gnathochilarium.

mentum A median plate or sclerite of the gnathochilarium; divided into anterior and posterior parts in Craspedosomatidae and Julidae.

mesomerite Middle part; an anterior part of the ninth pair of limbs in julid males which opposes the **promerite** (eighth pair) as a pair of pincers used to draw out the female vulvae.

metazonite The posterior, wider, part of the pleuro-tergal arch, with or without sternites incorporated, which overlaps the ring behind.

monozonian The condition of possessing a completely cylindrical sclerite of one piece, formed of fused tergite, pleurites and sternites (which may possess dorso-lateral expansions or paranota).

ocellus A single visual unit of the millipede eye, discernible externally as a convex lens; not homologous with the insect ocellus (*pl.* **ocelli**).

operculum The plate-like anterior sclerite of the vulva.

opisthocoelous The condition of certain vertebrate centra with a knob in front and a cavity behind.

opisthomerite Hind part; the posterior part of the modified ninth pair of legs in male julids, the gonopods proper.

oviposition The act of egg-laying.

ozadene The defence gland which secretes the repugnatorial chemical, situated in lateral pairs on rings VI to last in Julida, or on some of these in the Polydesmida, it is often visible through the transparent cuticle.

ozopore The opening of the defence gland or ozadene.

paragonopod Next to the gonopod; accessory to the gonopod proper.

paranotum Next to the shield (notum); a dorso-lateral or lateral extension of the posterior part of the tergite or pleurotergite (*pl.* **paranota**).

parthenogenesis Reproduction without male involvement; females lay unfertilized eggs which develop into females (in millipedes).

peltogonopods Accessory gonopods, often plate-like, protecting the gonopods proper.

penis A separate organ in Julida and Polyzoniida immediately behind the second pair of legs, carrying the male genital openings.

pentazonian With five zones of sclerotization in each trunk unit: a dorsal tergite, two lateral pleurites, and two sternites, one behind the other.

periodomorphosis A succession of stadia in some male Julida where a functional (copulatory) male moults into a non-functional regressed male (intercalary) and then moults again into a second copulatory stage.

phylacum An outer posterior leaf-like flange of the solenomerite of the julid gonopod, especially in Julini.

pitfall trap A jam jar or plastic beaker sunk into the soil with lip flush with the surface into which surface active animals blunder and are unable to escape up the smooth walls of the trap.

pleurite The sclerotized lateral part or pleuron of the trunk unit.

pleurotergite The fused tergite and lateral pleurites of a trunk unit; otherwise referred to as the pleurotergal arch.

pleurotergal arch See **pleurotergite.**

podomere The individual 'segment' or 'joint' of a leg.

podosternite The paragonopods (modified ninth limb pair) of *Craspedosoma.*

podous Bearing legs.

pre-anal ring The post-segmental ring which terminates the trunk; it may have a dorsomedian projection or tail; together with the anal valves and anal scale, forms the telson.

progoneate With genital openings anteriorly placed on the trunk (on the ring III).

proliferation zone The region between the last segment and the telson in which new segments are formed.

promerite *lit.* front part; anterior part of the julid gonopod (modified eighth leg) which protects the other parts when at rest, thus it is a peltogonopod, but also operates with the mesomerite as vulval extractor.

prostatic groove A channel in the gonopod in Polydesmida; called the sperm canal in older literature.

prozonite The anterior, narrower part of the trunk unit or ring which is overlapped by the metazonite of the ring in front.

pupoid Final embryonic stadium which hatches from the egg without externally visible appendages or segmentation; roughly similar to an insect pupa but by no means comparable.

rendzina A shallow soil formed on limestone or chalk.

ring A trunk unit consisting of a dorsal tergite, lateral pleurites and ventral sternites;

often fused together into a ring sclerite in Julida and Polydesmida; used instead of the word segment to avoid the need to distinguish the single segments I to IV from the diplosegments which follow.

row Of ocelli, added at each moult; if only one ocellus is added at each moult there is a single *line* of ocelli.

saprophagy Feeding on dead and decaying vegetable matter; similar to detritivory but allows the possibility that the animal is deriving nutrients from the organisms bringing about the decay.

secondary ramus An arm of the telopodite of a polydesmidan gonopod branching from the primary ramus and carrying the prostatic groove.

secondary sexual character A character associated with the sex of the individual other than the primary characters of the gonads and their ducts.

sclerite A part of the cuticle hardened for skeletal function (in millipedes calcification contributes to the hardening), distinct from the intervening cuticle which remains flexible to allow movement of one sclerite in relation to another.

sclerotized Hardened to form a sclerite, by a process of tanning of the protein of the cuticle; the millipede cuticle is hardened by tanning as well as the additional calcification; the condition is often wrongly described as 'chitinized'.

segment Strictly referring to the repeated units of the body produced serially along the axis of the embryo, or later in the proliferation zone, characterized by a pair of nerve ganglia and often by a pair of appendages or their rudiments.

semelparous Single laying; laying just one batch of eggs and then dying, or laying eggs in one breeding season only (*n.* **semelparity**).

seminal receptacle See **spermatheca.**

setation The arrangement or pattern of cuticular hairs or setae.

setose Bearing setae.

shield The second (and largest) tergite of a glomeridan or pill millipede; equivalent in function to the collum of a julidan.

solenomerite *lit.* tubular part; the tubular part of the opisthomerite of a julid carrying sperm channel and sometimes flagellum channel or groove; may be applied also to the posterior gonopod of a nemasomatid.

somatic As opposed to sexual.

spermatheca The apodematic pouch in the vulva of the female which receives sperm from a male partner and stores them until used to fertilize the eggs. Sometimes called **seminal vesicle.**

sperm canal The groove in the gonopod proper which conducts sperm to the apex of the organ.

stadium The part of the life history between two successive moults; the individual between two specified changes of skin or moults. *Synonym* of **instar** as used by most entomologists.

stadial spectrum The relative proportion of individuals in stated stadia at a given time.

stage The position of an individual in the developmental sequence, e.g. early stadia without secondary sexual characters are in a juvenile stage; a stage with sex apparent but still immature follows, and finally the mature male stage, or mature female, and sometimes an intercalary male stage.

A given stage, e.g. mature male, may occur in several different stadia in Julida where the concepts of stage and stadium are, to some degree, independent. In

Polydesmida the last stadium (VIII or VII) is usually the first and last mature stage and the two concepts are dependent.

stenotopic Narrow place; confined to a rather limited habitat. *Cf.* **eurytopic.**

sternite The hardened (sclerotized) ventral plate from which arise a pair of legs or their rudiments. In a diplosegment two individual sternites can be recognized, each with a pair of limbs and spiracles.

stipes The second (middle) of the three mandibular coxomeres which, together with the first (proximal) cardo, are visible externally as the cheek lobes; sometimes the stipes is not separated from the cardo (in Chordeumatida) (*pl.* **stipetes**).

sympatric *lit.* living together in the same country; sharing the same habitat or geographic area.

synanthropic *lit.* together with man; with a distribution closely related to human settlement or artefact.

syncolpocoxite The fused derivatives of the coxae of the gonopodal limbs; mentioned here only in the Brachychaeteumatidae.

telopod The end leg; the last enlarged legs of a male pill millipede (19th pair) used in mating; not to be confused with **telopodite** or with telopod used as a shortened form of telepodite.

telopodite The end part of the leg; a collective term for the podomeres of the leg distal to the coxa, i.e. trochanter, prefemur, femur, post femur, tibia, tarsus and claw, or of reduced derivatives of these.

telson The end part; the terminal part of the trunk posterior to the proliferation zone, and therefore post-segmental; consists of pre-anal ring, with or without caudal projection or tail, anal valves and subanal scale.

tergite Dorsal sclerite or plate of the trunk unit.

tribe An assemblage of genera below family and subfamily rank.

trichomes The hollow spines or setae of the bristly millipedes Polyxenida.

trivial name The second name of the binomial specific name, not in itself specific, but only when in combination with a generic name (e.g. the specific name *Ophyiulus pilosus* means 'hairy snake millipede', the trivial name means 'hairy').

trizonia The condition of the trunk unit with three separate plates or sclerites, a dorsal pleurotergite and two ventral sternites.

trunk The whole of the body behind the head; used for millipedes because there is no obvious distinction into thorax and abdomen (although rings I–IV, or I–III, have been called thoracic by some authors).

trunk unit A non-committal term to include both single and double segments of the trunk; synonymous with **ring.**

Tullgren funnel Apparatus designed by A. H. Tullgren for extracting animals from soil and litter. The sample is placed on a sieve and heat applied from above; animals move downwards away from the hot dry conditions and are directed by a funnel into a collecting vessel.

uniramous With a single unbranched telopodite, as distinct from the crustacean limb which may possess an outer exopodite and an inner endopodite.

vagile Actively wandering; usually implies much surface activity or above ground movement.

velum The anterior lobe of the opisthomerite in some Julini; the equivalent of the **brachit** of Cylindroiulini.

vice-county For the purpose of recording distribution we use a scheme designed many years ago by H. C. Watson; existing county boundaries are used but larger counties are subdivided into two (sometimes more) vice-counties, now being replaced by 10 Km and/or 50 Km grid.

vulva The organ behind the base of the second pair of legs of the female consisting of the sclerotized wall of the genital opening, principally the **bursa** and anterior **operculum.**

References

Bagnall, R. S. 1912a. New diplopods. *Rep. British Ass. Adv. Sci.* London **1912,** p. 42.

Bagnall, R. S. 1912b. *Chaetechylene vesuviana* and other myriapods new to the British fauna. *The Zoologist* **1912,** 264–266.

Bagnall, R. S. 1912c. Report of field meetings in 1911. *Trans. nat. Hist. Soc. Northumberland & Durham* **4,** 344–365.

Bagnall, R. S. 1913a. The myriapods of the Derwent Valley. *Trans. Vale of Derwent Nat. F.C.* (NS) **1** (2), 116

Bagnall, R. S. 1913b. Review of field work in 1911. *Entomologists' Record* **25** (9), 224–226.

Bagnall, R. S. 1916. A November week at Grange over Sands. II Woodlice and Myriapoda. *Lancs. Chesh. Nat.* **8,** 349.

Bagnall, R. S. 1917. On some Lancashire myriapods new to the British fauna. *Lancs. Chesh. Nat.* **10,** 104–109.

Bagnall, R. S. 1918. Records of some new British Diplopoda and Pauropoda with a preliminary check list of the British Myriapoda. *J. Zool. Research* **3,** 87–93.

Bagnall, R. S. 1919. On the discovery of two species of Brachychaeteumidae. *Ann. Mag. nat. Hist.* (9) **4,** 79–84.

Bagnall, R. S. 1922. On some new and rare British diplopods. *Ann. Mag. nat. Hist.* (9) **9,** 176–177.

Baker, A. N. 1974. Some aspects of the economic importance of millipedes. *Symp. zool. Soc. Lond.* No. **32,** 621–628.

Barber, A. D. 1969. Some Chilopoda and diplopod records from Northwest Essex. *Ent. mon. Mag.* **104,** 268.

Barber, A. D. and Daniel, R. 1975. *Leptoiulus kervillei* (*Brol.*) and *Chaetechylene vesuviana* from Devon. *Ent. mon. Mag.* **110,** 132.

Barber, A. D. and Fairhurst, C. P. 1974. A habitat and distribution recording scheme for Myriapoda and other invertebrates. *Symp. zool. Soc. Lond.* No. **32,** 611–619.

Barber, A. D. and Kime, R. D. 1971. Chilopoda and Diplopoda from Guernsey and Herm (Channel Isles). *Ent. mon. Mag.* **106,** 223.

Barber, A. D. and Kime, R. D. 1974. Some records of Chilopoda and Diplopoda from S. Wales. *Ent. mon. Mag.* **109,** 167.

Biernaux, J. 1969. Biotopes à *Schizophyllum sabulosum* L. *Bull. Rech. agron. Gembloux* NS **4** (1), 1–15.

Biernaux, J. 1972. Chorologie et étude biologique comparée de deux familles de Myriapodes-Diplopodes belges: les Blaniulidae et les Iulidae. Dissertation, Faculte des Sciences Agronomiques d'l'Etat, Gembloux.

Blower, J. G. 1952. British millipedes with special reference to Yorkshire species. *Naturalist* **1952,** 145–157.

Blower, J. G. 1953. On three species of *Cylindroiulus* Verhoeff in Britain. *Ann. Mag. nat. Hist.* (12) **6,** 305–316.

Blower, J. G. 1957. On some new and little-known British millipedes. *Ann. Mag. nat. Hist.* (12) **10,** 497–508.

Blower, J. G. 1958. British millipedes (Diplopoda). *Synopses Br. Fauna* No. **11,** pp. 74. Linnean Society, London.

Blower, J. G. 1969. Age structure of millipede populations in relation to activity and dispersion. *Syst. Ass. Publs.* No. **8,** 209–216.

Blower, J. G. 1970a. The millipedes of a Cheshire wood. *J. Zool., Lond.* **160,** 455–496.

Blower, J. G. 1970b. Notes on the life histories of some British Iulidae. *Bull. Mus. natn. Hist. nat. Paris* (2) **41,** Suppl. No. 2, 19–23.

Blower, J. G. 1972 The distribution of British millipedes as known at the end of 1969. *Bull. Br. My. Group* **1,** 9–38.

Blower, J. G. 1974a. Food consumption and growth in a laboratory population of *Ophyiulus pilosus* (Newport). *Symp. zool. Soc. Lond.* No. **32,** 527–551.

Blower, J. G. 1974b. The distribution of British millipedes as known up to 1970. *Symp. zool. Soc. Lond.* No. **32,** 603–609.

Blower, J. G. 1978. Anamorphosis in the Nematophora. *Abh. verh. naturwiss. ver. Hamburg* (NF) **21/22,** 97–103.

Blower, J. G. 1979. The millipede faunas of two British limestone woods. In Camatini, M. (Ed.) *Myriapod Biology*. London: Academic Press, 203-214.

Blower, J. G. and Gabbutt, P. D. 1964. Studies on the millipedes of a Devon oak wood. *Proc. zool. Soc. Lond.* **143,** 143–176.

Blower, J. G. and Fairhurst, C. P. 1968. Notes on the life-history and ecology of *Tachypodoiulus niger* in Britain. *J. Zool. Lond.* **156,** 257–271.

Blower, J. G. and Miller, P. F. 1974. The life-cycle and ecology of *Ophyiulus pilosus* (Newport) in Britain. *Symp. zool. Soc. Lond.* No. **32,** 503–525.

Blower, J. G. and Miller, P. F. 1977. The life history of the julid millipede *Cylindroiulus nitidus* in a Derbyshire wood. *J. Zool. Lond.* **183,** 339–351.

Blower, J. G. and Rolfe, S. W. 1956. *Metaiulus pratensis*, gen. et sp. nov., and *Leptoiulus kervillei* (Brolemann) from Britain. *Ann. Mag. nat. Hist.* (12) **9,** 513–520.

Blower, J. G. and Rundle, A. J. 1980. *Prosopodesmus panporus*, an interesting new species of polydesmoid millipede from the Royal Botanic Gardens, Kew, England. *Myriapodologica* **1** (4), 27–34.

Bocock, K. L., Heath, J. and Blower, J. G. 1973. Some observations on the biology of the millipede *Geoglomeris jurassica* Verhoeff, 1915. *J. nat. Hist.* **7,** 691–697.

Brade, H. K. and Birks, S. G. 1916. Notes on Myriapoda I. On a new variety of *Chordeumella scutellare* Ribaut. *Lancs. Ches. Nat.* (June 1916) **9,** 49–55.

Brade, H. K. and Birks, S. G. 1917a. V. On *Cylindroiulus (Leucoiulus) nitidus* (Verh.) *Ann. Mag. nat. Hist.* (8) **19,** 417–424.

Brade, H. K. and Brade-Birks, S. G. 1917b. VI. Report on Chilopoda and Diplopoda for 1916–1917. *Lancs. Ches. Nat.* (July 1917) **10,** 113–122.

Brade-Birks, H. K. and S. G. 1917c. VII. A new member of the Ascospermophora (*Iacksoneuma bradeae* gen. et sp. nov.). *J. Zool. Res.* **2** (4) 135–149.

Brade-Birks, H. K. and S. G. 1918a. X. On the family Brachychaeteumidae. *J. Zool. Res.* **3** (2 & 3), 47–53.

Brade-Birks, H. K. and S. G. 1918b. XI. Description of a new species of Diplopoda (*Brachychaeteuma melanops*). *J. Zool. Res.* **3** (2 & 3), 55–61.

Brade-Birks, H. K. and S. G. 1918c. XIII. Some Kent records. *Lancs. Ches. Nat.* (Dec. **1918**), 1–22.

Brade-Birks, H. K. and S. G. 1918d. XIV. The rediscovery of *Cylindroiulus parisiorum* (Brolemann and Verhoeff). *Ann. Mag. nat. Hist.* (9) **2,** 470–471.

Brade-Birks, S. G. 1920a. XXI. Colobognatha, an order of diplopods new to Britain represented by *Polyzonium germanicum* (Brandt). *Ann. Mag. nat. Hist.* (9) **5,** 198–200.

Brade-Birks, S. G. 1920b. XXIV. Preliminary note on a millipede new to science. *Ann. Mag. nat. Hist.* (9) **6,** 364–365.

Brade-Birks, H. K. and S. G. 1920c. XXV. Preliminary list for Lincolnshire and Norfolk. *Ann. Mag. nat. Hist.* (9) **6,** 470–477.

Brade-Birks, S. G. 1922. XXVI. The names of some Iulidae and Blaniulidae. *Ann. Mag. nat. Hist.* (9) **9,** 160–163.

Brade-Birks, S. G. 1930. XXXIII. The economic status of Diplopoda and Chilopoda and their allies. Part II. Diplopoda. *J. SE Agric. Coll. Wye, Kent* No. **27,** 103–146.

Brade-Birks, S. G. 1934. XXXV. Nomenclatorial Sources. *J. SE Agric. Coll. Wye, Kent.* **34,** 197–209.

Brade-Birks, S. G. 1939. XXXVI. Sources for description and illustration of the British fauna. *J. SE Agric. Coll. Wye, Kent* **44,** 156–179.

Brolemann, H. 1896. Matériaux pour servir a une Faune des Myriapodes de France. *Feuille J. Natural.* **26** (3) Nos. 306, 307, 115–119, 133–135.

Brolemann, H. 1913. Biospeologica XXXI. Gloмérides (Myriapodes). *Arch. Zool. expér. gén.* **52,** 387–445, pl. 15–19.

Brolemann, H. 1927. Myriapodes du Cirque de Gavarnie et notes sur les vulves de trois d'entre eux. *Bull. Soc. Hist. nat. Toulouse* **56.**

Brolemann, H. 1935. Diplopodes. *Faune de France,* **30,** 368 pp.

Brookes, C. H. 1963. Some aspects of the life-histories and ecology of *Proteroiulus fuscus* (Am Stein) and *Isobates varicornis* (C. L. Koch) with information on other blaniulid millipedes. Thesis: University of Manchester.

Brookes, C. H. 1974. The life-cycle of *Proteroiulus fuscus* (Am Stein) and *Isobates varicornis* (Koch) with notes on the anamorphosis of Blaniulidae. *Symp. zool. Soc. Lond.* No. **32,** 485–501.

Brookes, C. H. and Willoughby, J. 1978. An investigation of the ecology and life-history of the millipede *Blaniulus guttulatus* (Bosc) in a British woodland. *Abh. Verh. Naturwiss, Ver. Hamburg* (NF) **21/22,** 105–114.

Causey, N. B. 1943. Studies on the life-history and the ecology of the hothouse millipede *Orthomorpha gracilis* (C. L. Koch, 1847). *Amer. Mid. Nat.* **29** (3), 670–682.

Chamberlin, R. V. and Hoffman, R. L. 1958. *Checklist of the millipedes of North America.* U.S. National Museum Bull. No. **212,** pp. 1–236.

Chapman, P. 1979. The biology of Otterhole, near Chepstow. *B.C.R.A. Trans.* **6** (4), 159–167.

Cloudsley-Thompson, J. L. 1949. The enemies of Myriapoda. *Naturalist* **1949,** 137–141.

Cloudsley-Thompson, J. L. 1950. Economics of the spotted snake millipede *Blaniulus guttulatus* (Bosc). *Ann. Mag. nat. Hist.* (12) **3,** 1047–1057.

Cloudsley-Thompson, J. L. 1951. On the responses to environmental stimuli, and the sensory physiology of millipedes (Diplopoda). *Proc. zool. Soc. Lond.* **121,** 253–277.

Cotton, M. J. and Miller, P. F. 1974. A population of *Cylindroiulus latestriatus* (Curtis) on sand dunes. *Symp. zool. Soc. London.* No. **32,** 589–602.

Curtis, J. (1845) Observations on the natural history and economy of the insects called wireworms, etc. *J. Roy. Agric. Soc. Eng.* **5** (1), 180–237.

Davis, B. N. K. 1978. The ground arthropods of some chalk and limestone quarries in England. *J. Biogeography* **5,** 159–171.

Davis, B. N. K. 1979. The ground arthropods of London gardens. *The London Naturalist* **58,** 15–24.

Davis, B. N. K. 1982. Studies on the arthropod faunas of green urban ecosystems in Bornkamm, R., Lee, J. A. and Seaward, M. R. D. (Eds) *Urban Ecology,* Blackwell.

Demange, J.-M. 1958. Trois nouveaux myriapodes cavernicoles de France. *Notes Biospeol.* **13,** 51–56.

Demange, J.-M. 1965. Remarques sur quelque myriapodes cavernicoles de France: Description d'une forme nouvelle du genre *Metaiulus. Bull. Soc. Hist. nat. Toulouse* **100,** 446–450.

Demange, J.-M. 1970. Myriapodes Diplopodes de Madere et des Acores. *Bol. Mus. Mun. Funchal.* **25,** 5–43.

Demange, J.-M. 1981. *Les Milles-Pattes.* Paris, Boubée. pp. 288.

Deshmukh, I. 1974. In discussion of Cotton and Miller (1974).

Dohle, W. 1962. Der Brustschild der Plesioceraten (Diplopoda). *Zool. Anz.* **168,** 27–34.

Dohle, W. 1964. Die Embryonalentwicklung von *Glomeris marginata* (Villers) im Vergleich zur Entwicklung anderer Diplopoden. *Zool. Jb.* (*Anat.*). **81,** 241–310.

Dohle, W. 1974. The segmentation of the germ band of Diplopoda compared with other classes of arthropods. *Symp. zool. Soc. London* **32,** 143–161.

Eason, E. H. 1957. Chilopoda and Diplopoda from Caernarvonshire. *Proc. zool. Soc. Lond.* **129,** 273–291.

Edwards, E. E. 1929. A survey of the insect and other invertebrate fauna of arable land. *Ann. appl. Biol.* **16,** 299–323.

Eisner, T., Alsop, D., Hicks, K. and Meinwald, J. 1978. Defensive secretions of millipedes *in* Bettini, Sergio (Ed) *Arthropod Venoms.* Springer-Verlag. pp. 41–72. (Handbook of Experimental Pharmacology **48**).

Enghoff, H. 1974. Om tusindbenenes ud bredelse i Danmark. (English summary: On the distribution of millipedes in Denmark). *Ent. Meddr.* **42,** 21–32.

Enghoff, H. 1976a. Competition in connection with geographic parthenogenesis: Theory and examples, including some original observations on *Nemasoma varicorne* C. L. Koch. *J. nat. Hist.* **10,** 475–479.

Enghoff, H. 1976b. Morphological comparison of bisexual and parthenogenetic *Polyxenus lagurus* (Linné, 1758) in Denmark and Southern Sweden, with notes on taxonomy, distribution and ecology. *Ent. Meddr.* **44,** 161–182.

Enghoff, H. 1976c. Parthenogenesis and bisexuality in the millipede *Nemasoma varicorne* C. L. Koch, 1847. Morphological, ecological and biogeographical aspects. *Vidensk. Meddr. dansk naturh. Foren.* **139,** 21–59.

Enghoff, H. 1978a. Parthenogenesis and bisexuality in the millipede *Nemasoma varicorne* C. L. Koch, 1847. II. Distribution, substrate and abundance of the bisexual and thelytokous form in some Danish forests. *Ent. Meddr.* **46,** 73–79.

Enghoff, H. 1978b. Parthenogenesis and spanandry in millipedes. *Abh. Verh. naturwiss. Ver. Hamburg* (NF) **21/22,** 73–85.

Enghoff, H. and Shelley, 1979. A revision of the millipede genus *Nopoiulus. Ent. Scand.* **10,** 65–72.

Evans, William 1900. Scottish Myriapoda. *Ann. Scot. Nat. Hist.* **1900,** 127.

Evans, William 1907. The Myriapoda of the Forth area. *Proc. Roy. Phys. Soc. Edin.* **16,** 405–414 and **17,** 109–120.

Fairhurst, C. P. 1968. *Life cycles and activity patterns in schizophylline millipedes.* Thesis; University of Manchester.

Fairhurst, C. P. 1970. Activity and wandering in *Tachypodoiulus niger* (Leach) and *Schizophyllum sabulosum* (Linne). *Bull. Mus. natn. Hist. nat. Paris* (2) **41,** Suppl. No. 2, 61–66.

Fairhurst, C. P. 1974. The adaptive significance of variations in the life cycles of schizophylline millipedes. *Symp. zool. Soc. Lond.* No. **32,** 575–587.

Fairhurst, C. P. 1979. The distribution of millipedes on a Lincolnshire sand dune system. In Camatini, M. (Ed.) *Myriapod Biology*. London, Academic Press, 241–249.

Fairhurst, C. P. and Armitage, M. L. 1979. The British myriapod survey 1978. In Camatini, M. (Ed.) *Myriapod Biology.* London, Academic Press, 183–194.

Fairhurst, C. P. and Barber, A. D. 1972. British Myriapod Survey. *Bull. Br. My. Group* **1,** 5.

Fairhurst, C. P., Barber, A. D. and Armitage, M. L. 1978. The British myriapod survey – April 1975. *Abh. Verh. naturwiss. Ver. Hamburg* (NF) **21/22,** 129–134.

Foster, N. H. 1919. A list of the myriapods of Ulster. *Ann. Mag. nat. Hist.* (9) **4,** 395–407.

Fussey, G. D. and Varndell, I. M. 1980. The identification of the sexual form of the bristly millipede, *Polyxenus lagurus* (Linné, 1758) at three coastal sites in England and Wales, using sex ratios. *Naturalist,* **105,** 151–154.

Haacker, U. 1964. Das Paarungsverhalten des Saftkuglers *Glomeris marginata. Natur. Mus., Frankf.* **94,** 265–272.

Haacker, U. 1968. Deskriptive, experimentelle und vergleichende untersuchungen zur Autokologie rhein-mainischer Diplopoden. *Oecologia* **1,** 87–129.

Haacker, U. 1969a. Spermaübertragung von *Glomeris* (Diplopoda). *Naturwissenschaften* **56,** 467.

Haacker, U. 1969b. An attractive secretion in the mating behaviour of a millipede. *Z. Tierpsychol.* **26,** 988–990.

Haacker, U. 1970. Experimentelle Untersuchungen zur Ökologie von *Unciger foetidus* (C. L. Koch). *Bull. Mus. Hist. nat. Paris* (2) **41** (Suppl. 2), 67–71.

Haacker, U. 1971. Die Funktion eines dorsalen Drüsenkomplexes im Balzverhalten von *Chordeuma. Forma et functio* **4,** 162–170.

Halkka, R. 1958. Life history of *Schizophyllum sabulosum* (L). *Suomal. elain-ja kasvit. Seur. Van. elain. Julk.* **19** (4), 1–72.

Harding, P. T. 1985. Recent records of *Thalassisobates littoralis* (Silvestri). *Bull. Br. My. Gp.* **2,** 6–7.

Haupt, J. 1979. Phylogenetic aspects of recent studies on myriapod sense organs. In Camatini, M. (Ed.) *Myriapod Biology.* Academic Press, 391–406.

Hazelton, M. and Glennie, E. A. 1962. Cave fauna and flora. In Cullingford, C. H. D. (Ed.) *British Caving: An introduction to speleology.* Cave Research Group. Routledge & Kegan Paul, London. 2nd. Edn. pp. 347–395.

Heath, J., Bocock, K. L. and Mountford, M. D. 1974. The life history of the millipede *Glomeris marginata* (Villers) in north-west England. *Symp. zool. Soc. Lond.* No. **32,** 433–462.

Hoffman, R. S. 1979. *Classification of the Diplopoda.* Museum d'Histoire Naturelle, Geneve. pp. 237.

Jackson, A. R. 1914. Myriapoda of the Chester district. *Lancashire Naturalist* **6,** 450.

Jackson, A. R. 1915. On some arachnids and myriapods observed in 1914. *Lancs. Ches. Nat.* **7,** 433.

Jackson, A. R. 1916. On some arthropods observed in 1915. *Lancs. Ches. Nat.* **8,** 391.

Jackson, Noel 1982. The millipedes, centipedes and woodlice of Castle Eden Dene. *Vasculum* **67** (3), 41–47.

Jeekel, C. A. W. 1968. The generic and sub generic names of the European julid generally referred to as *Schizophyllum* (Verhoeff, 1895). *Ent. Ber., Amst.* **28,** 49–51.

Jeekel, C. A. W. 1971. *Nomenclator generum et familiarum Diplopodorum.* A list of the genus and family-group names in the class Diplopoda from the 10th edition of Linneus, 1758, to the end of 1957. Amsterdam.

Jeekel, C. A. W. 1973. *Julus scandinavius* Latzel, a millipede new to U.S. fauna. *Ent. Ber., Amst.* **33,** 101–102.

Jeekel, C. A. W. 1978. Voorlopige atlas van de verspreiding der Nederlandse Miljoenpoten. *Verslagen en Technische gegevens.* Instituut voor Taxonomische Zöologie. Universiteit van Amsterdam. No. **15.**

Johnson, W. F. 1913. Notes on Irish Myriapoda. *Irish Naturalist* **22,** 128–130.

Johnson, W. F. 1915. Chilopoda and Diplopoda. Clare Island survey. *R. I. A. Proc.* **31,** 33.

Johnston, G. 1835. Insecta Myriapoda found in Berwickshire. *Mag. Nat. Hist.* **8,** 486–494.

Jones, R. E. 1985. *Unciger foetidus*, a millipede new to Britain from Norfolk. *Trans. Norfolk & Norwich Nat. Soc.* **27,** 63–65.

Kayed, Ahmed N. 1978. Consumption and assimilation of food by *Ophyiulus pilosus* (Newport). *Abh. Verh. naturwiss. Ver. Hamburg* (NF) **21/22,** 121–128.

Kheirallah, A. M. 1966. *Studies on the feeding behaviour of the millipede* Iulus scandinavius *Latzel, 1884.* Thesis: University of Manchester.

Kheirallah, A. M. 1979. Behavioural preference of *Iulus scandinavius* to different species of leaf litter. *Oikos* **33,** 466–471.

Kime, R. D. 1968. A rare millipede, *Entothalassinum italicum* (Latzel) in Surrey. *Ent. mon. Mag.* **104,** 95.

Kime, R. D. 1978. The diustribution of millipedes in the south of England. A preliminary survey. *Abh. Verh. naturwiss. Ver. Hamburg.* (NF) **21/22,** 135–147.

Kinkel, H. 1955. Zur biologie und Okologie des getupfelten Tausendfusses *Blaniulus guttulatus* Gerv. *Z. angew. Ent.* **37,** 401–436.

Lang, J. 1954. Mnohozky – Diplopoda. *Fauna CSR* **2,** 1–183.

Lang, J. 1959. Einige Bemerkungen zur Okologie von *Orthomorpha gracilis* C. L. Koch, und zu ihrem Vorkommen in Prager Glashausern. *Vest. cs. zool. spolecnosti* **23** (2), 97–122.

Langton, P. 1968. Four millipedes new to Cambridgeshire and confirmation of *Ophyiulus pilosus* (Newport) for the county. *Ent. mon Mag.* **104,** 109.

Latzel, R. 1884. *Die Myriapoden der osterreichisch-ungarischen Monarchie.* Wien: Holder. **2,** 1–14.

Leach, W. E. 1815. A tabular view of the external characters of four classes of animals which Linné arranged under Insecta. *Trans. Linn. Soc. London* **11,** 306–400.

Lokšina, I. E. and Golovatch, S. I. 1979. Diplopoda of the USSR fauna. *Pedobiologia* **19,** 381–389.

Lewis, J. G. E. 1972. On the nature of 'intercalary' males in *Brachydesmus superus* (Latzel). *Ent. mon. Mag.* **107,** 158–159.

Lindroth, C. H. 1957. *The faunal connections between Europe and North America.* Stockholm: Almquist & Wiksell.

Lohmander, H. 1925. Sverigers Diplopoder. *Götesborgs K. vet-vit-samhähandl.* (4) **30,** 1–115.

Lyford, W. H. Jnr. 1943. The palatability of freshly fallen forest tree leaves to millipedes. *Ecology* **24,** 252–261.

Manton, S. M. 1950. The Evolution of Arthropodan Locomotory Mechanisms. Part 1. The locomotion of *Peripatus. J. Linn. Soc. (Zool.)* **41,** 529–70.

Manton, S. M. 1952a. The Evolution of Arthropodan Locomotory Mechanisms. Part 2. General Introduction to the Locomotory Mechanisms of the Arthropoda. *J. Linn. Soc. (Zool.)* **42,** 93–117.

Manton, S. M. 1952b. The Evolution of Arthropodan Locomotory Mechanisms. Part 3. The Locomotion of the Chilopoda and Pauropoda. *J. Linn. Soc. (Zool.)* **42,** 118–67.

Manton, S. M. 1954. The evolution of arthropod locomotory mechanisms. Part 4: The structure, habits and evolution of the Diplopoda. *J. Linn. Soc. Lond. (Zool.)* **42,** 299–368.

Manton, S. M. 1956. The evolution of arthropod locomotory mechanisms. Part 5: The structure, habits and evolution of the Pselaphognatha (Diplopoda). *J. Linn. Soc. Lond. (Zool.)* **43,** 153–187.

Manton, S. M. 1958. The evolution of arthropod locomotory mechanisms. Part 6. Habits and evolution of the Lysiopetaloidea (Diplopoda), some principles of leg design in Diplopoda and Chilopoda, and limb structure in Diplopoda. *J. Linn. Soc. Lond. (Zool.)* **43,** 489–556.

Manton, S. M. 1972. The evolution of arthropodan locomotory mechanisms. Part 10. Locomotory habits, morphology and evolution of the hexapod classes. *Zool. J. Linn. Soc.* **51,** 203–400.

Manton, S. M. 1973. The evolution of arthropodan locomotory mechanisms. Part 11. Habits, morphology and evolution of the Uniramia (Onychophora, Myriapoda, Hexapoda) and comparisons with the Arachnida, together with a functional review of uniramian musculature. *Zool. J. Linn. Soc.* **53,** 257–375.

Manton, S. M. 1977. *The Arthropoda: habits, functional morphology and evolution.* Oxford: Clarendon Press 527 pp.

Mauriès, J.-P. 1960. Une nouvelle espèce pyrénéene du genre *Adenomeris. Bull. Soc. Hist. nat. Toulouse* **95,** 401–404.

Mauriès, J.-P. 1964. Notes sur les diplopodes Pyrénéns I. Les *Cylindroiulus* du sous-genre *Bracheoiulus* Verhoeff. *Bull. Soc. Hist. nat. Toulouse* **99,** 444–449.

Mauriès, J.-P. 1965. Une nouvelle sous-espece cavernicole de *Metaiulus pratensis* Blower & Rolfe, 1956. *Ann. Speleologie* **20,** 519–522.

Meidell, B. A. 1968, *Microchordeuma gallicum* (Latzel 1884) new to Scandinavia. *Norsk. ent. Tidsskr.* **15,** 41–46.

Meidell, B. A. 1970. On the distribution, sex ratio, and development of *Polyxenus lagurus* (L) in Norway. *Norsk. ent. Tidsskr.* **17,** 147–152.

Miller, P. F. 1974. Competition between *Ophyiulus pilosus* (Newport) and *Julus scandinavius* Latzel. *Symp. zool. Soc. Lond.* No. **32,** 553–574.

Morris, H. M. 1922. The insect and other invertebrate fauna of arable land at Rothamsted. *Ann. appl. Biol.* **9,** 282–305.

Morris, H. M. 1927. The insect and other invertebrate fauna of arable land at Rothamsted. Part II. *Ann. appl. Biol.* **14,** 442–464.

Nelson, J. M. 1964. *Chordeuma proximum* Ribaut, a millipede new to Britain. *Ann. Mag. nat. Hist.* (13) **7,** 527–528.

Newport, G. 1844. Description of a new British *Julus. Ann. Mag. nat. Hist.* (1) **11,** 316.

Nguyen Duy-Jacquemin, M. 1976. Étude de la variabilité des caractères de deux espèces du genre *Polyxenus, P. lagurus* L et *P. fasciculatus* Say. *Bull. Mus. nat. Hist. nat.* (3) No. 356 *Zool.* **249,** 105–118.

Palmen, E. 1949. The Diplopoda of Eastern Fennoscandia. *Suomal. elain-ja kasvit. Seur. van elain Julk* **13** (6), 1–54.

Pearson, R. G. and White, E. 1964. The phenology of some surface active arthropods of moorland country in North Wales. *J. Anim. Ecol.* **33,** 245–258.

Peitsalmi, Maija 1981. Population structure and seasonal changes in activity of *Proteroiulus fuscus* (Am Stein). *Acta Zoologica Fennica* **161,** 1–66.

Petersen, A. C. 1975. A review of the distribution of Irish millipedes. *Proc. Roy. Irish Acad.* **75,** 569–583.

Pocock, R. I. 1893. Notes upon some Irish Myriapoda. *Irish Naturalist* **11,** 309–312.

Pocock, R. I. 1900. On two English millipedes (*Iulus londinensis* Leach, *Iulus teutonicus* sp. n.). *Ann. Mag. nat. Hist.* (7) **6,** 206–207.

Pocock, R. I. 1901. Myriapoda in *Vict. History, County of Cumberland* **1,** 193–195.

Pocock, R. I. 1902. Myriapoda in *Vict. History, County of Surrey* **1,** 176–178.

Pocock, R. I. 1903. Myriapoda in *Vict. History, County of Essex* **1,** 193–195.

Pocock, R. I. 1906. Myriapoda in *Vict. History, County of Somerset* **1,** 000–000.

Pocock, R. I. 1906. The wild fauna and flora of the Royal Botanic Gardens, Kew. *Antennata* Kew Bull Add. Sec 5 (**1906**) 21–22.

Rantala, Maija 1970. Anamorphosis and periodomorphosis of *Proteroiulus fuscus* (Am Stein). *Bull. Mus. natn. Hist. nat. Paris* (2) **41** Suppl. No. 2, 122–128.

Rantala, Maija 1974. Sex ratio and periodomorphosis of *Proteroiulus fuscus* (Am Stein). *Symp. zool. Soc. Lond.* No. **32,** 463–469.

Remy, Paul A. 1950. On the enemies of Myriapoda. *Naturalist* **1950,** 103–108.

Ribaut, H. 1905. Notes myriopodologiques I. *Bull. Soc. Hist. nat. Toulouse* **38,** 3–7.

Ribaut, H. 1909. Nouveau genre de Glomeroidea. *Bull. Soc. Hist. nat. Toulouse* **42,** 29–32.

Rolfe, S. W. 1934. Notes on Diplopoda I. The re-study of a widely distributed British millipede *Ophyiulus pilosus* (Newport). *Ann. Mag. nat. Hist.* (10) **14,** 192–203.

Rolfe, S. W. 1935. Notes on Diplopoda II. On one of the rarer of the British Polydesmidae (*Polydesmus testaceus* C. L. Koch). *Ann. Mag. nat. Hist.* (10) **15,** 284–290.

Rolfe, S. W. 1937. Notes on Diplopoda IV. The recognition of some millipedes of economic importance. *Journ. S.E. Agric. Coll. Wye, Kent* **40,** 99–107.

Rolfe, S. W. 1938. Notes on Diplopoda V. The recognition of some millipedes of economic importance. *Journ. S.E. Agric. Coll. Wye, Kent* **42,** 214–215.

Rolfe, S. W. 1939. Notes on Diplopoda VI. The recognition of some millipedes of economic importance. *Journ. S.E. Agric. Coll. Wye, Kent* **44,** 180–182.

Sahli, F. 1955. Presence en Sarre et contribution à l'étude du développement post-embryonnaire de *Cylindroiulus (Aneuloboiulus) silvarum* Meinert 1868. *Ann. Univ. saraviensis Sci.* **4,** 151–164.

Sahli, F. 1969a. Existence d'une succession adulte-adulte chez les males du diplopod *Cylindroiulus nitidus* (Verhoeff). La question de males *rhenanus. C. r. hebd. Seanc. Acad. Sci., Paris* **269,** 2254–2257.

Sahli, F. 1969b. Contribution à l'étude du développement post-embryonnaire des Diplopodes Iulides. *Ann. Univ. saraviensis, Sci.* **7,** 1–154.

Sahli, F. 1973. Periodomorphose, mues post-imaginales particulère chez un diplopod du sol: *Cylindroiulus nitidus* (Verhoeff). *Annls. Soc. r. zool. Belg.* **103,** 147–155.

Sahli, F. 1978. Remarques sur le développement post-embryonnaire de *Tachypodoiulus albipes* (C. L. Koch) et sur la variabilité du nombre des anneaux apodes terminaux. *Abh. Verh. naturwiss. Ver. Hamburg* (N.F.) **21/22,** 121–128.

Sahli, F. 1982. Presence de males *rhenanus* en Grande-Bretagne che le Diplopode *Cylindroiulus nitidus* (Verhoeff) et remarques sur les intercalaires de cette espece. *Bull. sci. Bourg.* **35** (1): 37–42.

Saudray, Y. 1952. Dévelopement post-embryonnaire d'un Iulide indigene *Cylindroiulus (Aneuloboiulus) silvarum* Meinert *Archs. Zool. exp. gén. (Notes Rev.)* **89,** 1–14.

Schömann, K. 1956. Zur biologie von *Polyxenus lagurus* (L, 1758). *Zool. Jb. (Syst.)* **84,** 195–256.

Schubart, O. 1930. *Brachychaeteuma verhoeffi* nov. spec., ein neuer deutscher Diplopode. *Zool. Anz.* **90,** 38–45.

Schubart, O. 1934. Diplopoda. *Tierwelt Dtl.* **28,** 1–318.

Schubart, O. 1938. Ein für Deutschland neuer Diplopode aus westdeutschen Höhlen. *Sonderdruck aus den Mitteilungen uber Höhlen und Karstforschung* **1938,** 133–137.

Schubart, O. 1957. Die Diplopoden der Mark Brandenberg. *Mitt. Zoo. Museum Berlin* **33** (1): 4–94.

Schubart, O. and Husson, R. 1937. Les diplopodes de cavités souterraines du Nord-Est de la France. *Bull. Soc. Zool. France.* **61,** 484–502.

Selbie, C. M. 1913. New records of Irish Myriapods. *Irish Naturalist* **22,** 131–135.

Snider, R. M. 1981a. Diplopoda as food for Coleoptera: Laboratory experiments. Paper to 5th International Congress of Myriapodology Radford, Virginia.

Snider, R. M. 1981b. Growth and survival of *Polydesmus inconstans* (Diplopoda: Polydesmidae) at constant temperatures. *Pedobiologia* **22,** 345–353.

Snider, R. M. 1981c. The reproductive biology of *Polydesmus inconstans* (Diplopoda: Polydesmidae) at constant temperatures. *Pedobiologia* **22,** 354–365.

Stephenson, J. W. 1961. The biology of *Brachydesmus superus* (Latzel). *Ann. Mag. nat. Hist.* (13) **3,** 311–319.

Thomas, Mary 1982. Unusual outing. (Letter to Editor.) *Birds.* Royal Society for the Protection of Birds. **9** (4), 63.

Turk, F. A. 1944. Myriapoda (Chilopoda and Diplopoda) from Cornwall with notes and descriptions of forms new to the British fauna. *Ann. Mag. nat. Hist.* (11) **11,** 532–551.

Turk, F. A. 1947. Myriapodological notes II. Northwest. Nat. **1947,** 226–234.

Vachon, M. 1947. Contribution à l'étude de dévelopement post-embryonnaire de *Pachyiulus ligulatus* Voges. Les etapes de la croissance. *Annls. Sci. nat. (Zool.)* (11) **9,** 109–121.

Vandel, A. 1926. La Spanandrie (disette de males) geographique chez le Myriapode (*Polyxenus lagurus* L). *C. r. hebd. Seanc. Sci., Paris* **182,** 1100–1102.

Verhoeff, K. W. 1911. Uber *Brachychaeteuma* n.g. und *Titanosoma jurassicum* aus England. *Zool. Anz.* **38,** 455–458.

Verhoeff, K. W. 1912. On the occurrence of *Brachychaeteuma, Titanosoma* and *Polymicrodon* in England. *Trans. Nat. Hist. Soc. Northumberland, Durham & Newcastle-upon-Tyne* **4,** 143–167.

Verhoeff, K. W. 1915. Zur kenntnis der Plesiocerata. *Zool. Anz.* **46,** 16–29, 43–62.

Verhoeff, K. W. 1925. Neuer Diplopoden Beiträge. *Zool. Jahb. Abt. Syst.* **50,** 61–122, pl. 2–4.

Verhoeff, K. W. 1928. Diplopoda I *Bronn's Kl. Ordn. Tierreichs* **5** (2), 1–1072.

Verhoeff, K. W. 1933. Wachstum und Lebensverlangerung bei Blaniuliden und uber die Periodomorphose. *Zool. Anz.* **108,** 27–40.

Verhoeff, K. W. 1939. Wachstum und Lebensverlangerung bei Blaniuliden und uber die Periodomorphose. *Zschr. Morphol. Okol. Tiere* **36,** 21–40.

van der Drift, J. 1951. Analysis of the animal community in a beech forest floor. *Meded. Inst. toegep. biol. Onderz. Nat.* **9,** 1–168.

Waga, M. A. F. 1839. Observations sur les myriapodes. *Revue zoologique* **1839,** 76–90.

Yalden, D. W. 1976. The food of the hedgehog in England. *Acta theriol.* **21,** 401–424.

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