THE

CAMBRIDGE NATURAL HISTORY

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VOLUME IV

CRUSTACEA

By GEOFFREY SMITH, M.A. (Oxon.), Fellow of New College, Oxford; and the late W. F. R. WELDON, M.A. (D.Sc., Oxon.), formerly Fellow of St. John's College, Cambridge, and Linacre Professor of Human and Comparative Anatomy, Oxford

TRILOBITES

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INTRODUCTION TO ARACHNIDA, AND KING-CRABS

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EURYPTERIDA

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SCORPIONS, SPIDERS, MITES, TICKS, ETC.

By CECIL WARBURTON, M.A., Christ's College, Cambridge; Zoologist to the Royal Agricultural Society

TARDIGRADA (WATER-BEARS)

By A. E. SHIPLEY, M.A., F.R.S., Fellow and Tutor of Christ's College, Cambridge; Reader in Zoology

PENTASTOMIDA

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PYCNOGONIDA

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APPENDICES TO ARACHNIDA

I. AND II

TARDIGRADA AND PENTASTOMIDA

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CHAPTER XIX

TARDIGRADA

OCCURRENCE—ECDYSIS—STRUCTURE—DEVELOPMENT—AFFINITIES—BIOLOGY—DESICCATION—PARASITES—SYSTEMATIC

THE animals dealt with in this chapter lead obscure lives, remote from the world, and few but the specialist have any first-hand acquaintance with them. Structurally they are thought to show affinities with the Arachnida, but their connexion with this Phylum is at best a remote one.

Tardigrades are amongst the most minute multicellular animals which exist, and their small size—averaging from $\frac{1}{2}$ to 1 mm. in length—and retiring habits render them very inconspicuous, so that as a rule they are overlooked; yet Max Schultze[1] asserts that without any doubt they are the most widely distributed of all segmented animals. They are found amongst moss, etc., growing in gutters, on roofs, trees or in ditches, and in such numbers that Schultze states that almost any piece of moss the size of a pea will, if closely examined, yield some members of this group, but they are very difficult to see. The genus *Macrobiotus* especially affects the roots of moss growing on stones and old walls. *M. macronyx* lives entirely in fresh water, and *Lydella dujardini* and *Echiniscoides sigismundi* are marine; all other species are practically terrestrial, though inhabiting very damp places.

In searching amongst the heather of the Scotch moors for the ova and embryos of the Nematodes which infest the alimentary canal of the grouse, I have recently adopted a method not, as far as I am aware, in use before, and one which in every

[1] *Arch. mikr. Anat.* Bd. i., 1865, p. 428.

case has yielded a good supply of Tardigrades otherwise so difficult to find. The method is to soak the heather in water for some hours and then thoroughly shake it, or to shake it gently in a rocking machine for some hours. The sediment is allowed to settle, and is then removed with a pipette and placed in a centrifugaliser. A few turns of the handle are sufficient to

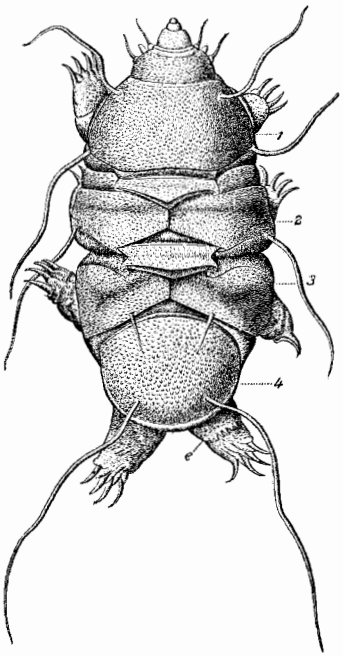

FIG. 249.—Dorsal view of *Echiniscus testudo*, C. Sch., × 200, showing the four segments 1, 2, 3, 4. (From Doyère.)

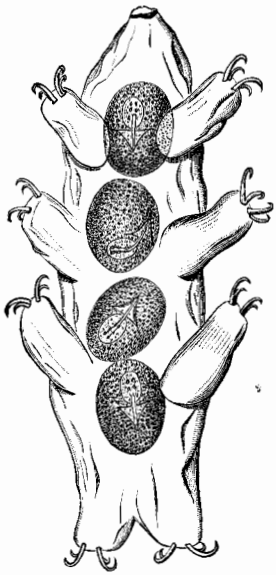

FIG. 250.—Cast-off cuticle of *Macrobiotus tetradactylus*, Gr., × about 150, containing four eggs in which the boring apparatus of the embryo can be distinguished. (From R. Greeff.)

concentrate at the bottom of the test-tubes a perfectly amazing amount of cryptozoic animal life, and amongst other forms I have never failed to find Tardigrades.

Many Tardigrades are very transparent; their cells are large, and arranged in a beautifully symmetrical manner; and since those of them that live in moss, and at times undergo desiccation, are readily thrown into a perfectly motionless state, during which they may be examined at leisure, it is not surprising that these little creatures have been a favourite object

for histological research. One way to produce the above-mentioned stillness is partly to asphyxiate the animals by placing them in water which has been boiled, and covering the surface of the water with a film of oil.

The whole body is enclosed in a thin transparent cuticle, which must be pierced by a needle if it be desired to stain the tissues of the interior. As a rule the cuticle is of the same thickness all over the body, but in the genus *Echiniscus* the cuticle of the dorsal surface is arranged in thickened plates, and these plates are finely granulated. From time to time the cuticle is cast, and this is a lengthy process, so that it is not unusual to find a Tardigrade ensheathed in two cuticles, the outer of which is being rubbed off. The Macrobioti lay their eggs in their cast cuticle (Fig. 250). The end of each of the eight legs bears forked claws of cuticular origin. The legs are not jointed except in the genus *Lydella,* where two divisions are apparent.

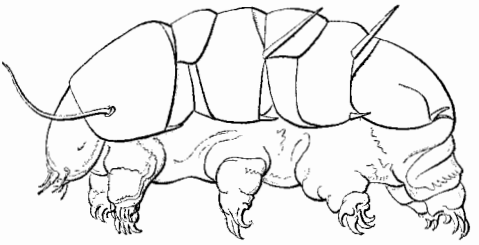

FIG. 251.—*Echiniscus spinulosus*, C. Sch., × about 200, seen from the side. (From Doyère.)

Within the cuticle is the epidermis, a single layer of cells arranged in regular longitudinal and transverse rows along the upper and under surface, where the cells are as uniformly arranged and as rectangular as bricks. The cells on the sides of the body are polygonal, and not in such definite rows. The nuclei show the same diagrammatic symmetry as the cells which contain them, and lie in the same relative position in neighbouring cells. In a few places, such as the end of each limb and around the mouth and arms, the cells of the epidermis are heaped up and form a clump or ridge. In some genera a deposit of pigment in the epidermis, which increases as the animal grows old, obscures the internal structures. It is generally brown, black, or red in colour.

The cuticle and epidermis enclose a space in which the various internal organs lie. This space is traversed by numerous symmetrically disposed muscle-fibres, and contains a clear fluid—the blood—which everywhere bathes these organs. This fluid

evaporates when desiccation takes place, and is soon replaced after rain; it forms no coagulum when reagents are added to it, and it probably differs but little from water. Floating in it are numerous corpuscles, whose number increases with age. In well-fed Tardigrades the corpuscles are packed with food-reserves, often of the same colour—green or brown—as the contents of the stomach, which soon disappear when the little creatures are starved.

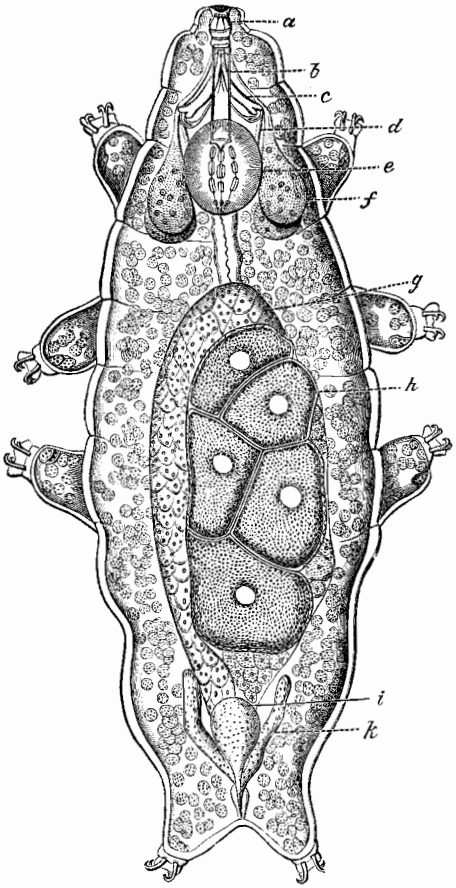

FIG. 252. — *Macrobiotus schultzei*, Gr., × 150. (Modified from Greeff.) *a*, The six inner papillae of the mouth; *b*, the chitin-lined oesophagus; *c*, calcareous spicule; *d*, muscle which moves the spicule; *e*, muscular pharynx with masticating plates; *f*, salivary glands; *g*, stomach; *h*, ovary; *i*, median dorsal accessory gland; *k*, diverticula of rectum.

The alimentary canal begins with an oral cavity, which is in many species surrounded by chitinous rings. The number of these rings and their general arrangement are of systematic importance. The oral cavity opens behind into a fine tube lined with chitin, very characteristic of the Tardigrada, which has been termed the mouth-tube. By its side, converging anteriorly, lie the two chitinous teeth, which may open ventrally into the mouth-tube, as in *Macrobiotus hufelandi* and *Doyeria simplex*, or may open directly into the oral cavity, as in *Echiniscus*, *Milnesium*, and some species of *Macrobiotus*. In some of the last named the tips of the teeth are hardened by a calcareous deposit. The hinder end of each stylet or tooth is

supported by a second chitinous tooth-bearer,[1] and the movement of each is controlled by three muscles, one of which, running forwards to the mouth, helps to protrude the tooth, whilst the other two running upwards and downwards to the sheath of the pharynx, direct in what plane the tooth shall be moved.

The mouth-tube passes suddenly into the muscular sucking pharynx, which is pierced by a continuation of its chitinous tube. Roughly speaking, the pharynx is spherical; the great thickness of its walls is due to radially arranged muscles which run from the chitinous tube to a surrounding membrane. When the muscles contract, the lumen of the tube is enlarged, and food, for the most part liquid, is sucked in. Two large glands, composed of cells with conspicuous nuclei, but with ill-defined cell outlines, pour their contents into the mouth in close proximity to the exit of the teeth. The secretion of the glands—often termed salivary glands—is said in many cases to be poisonous.

The pharynx may be followed by a distinct oesophagus, or it may pass almost immediately into the stomach, which consists of a layer of six-sided cells arranged in very definite rows. In fully-fed specimens these cells project into the lumen with a well-rounded contour. Posteriorly the stomach contracts and passes into the narrow rectum, which receives anteriorly the products of the excretory canals and the reproductive organs, and thus forms a cloaca. Its transversely-placed orifice lies between the last pair of legs. The food of Tardigrades is mainly the sap of mosses and other humble plants, the cell-walls of which are pierced by the teeth of the little creatures.

The organs to which an excretory function has been attributed are a pair of lateral caeca, which vary much in size according as the possessor is well or ill nourished. They recall the Malpighian tubules of such Mites as *Tyroglyphus*. Nothing comparable in structure to nephridia or to coxal glands has been found.

The muscles show a beautiful symmetry. There are ventral, dorsal, and lateral bundles, and others that move the limbs and teeth, but the reader must be referred to the works of Basse, Doyère,[2] and Plate[3] for the details of their arrangement. The muscle-fibres are smooth.

[1] A. Basse, *Zeitschr. wiss. Zool.* lxxx., 1906, p. 259.

[2] *Ann. Sci. nat.* (2), xiv., 1840, p. 269, and xvii., 1842, p. 193.

[3] *Zool. Jahrb. Anat.* iii., 1889. This paper contains a bibliography.

The nervous system consists of a brain or supra-oesophageal ganglion, whose structure was first elucidated by Plate, and a ventral chain of four ganglia. Anteriorly the brain is rounded, and gives off a nerve to the skin; posteriorly each half divides into two lobes, an inner and an outer. The latter bears the eye-spot when this is present. Just below this eye a slender nerve passes straight to the first ventral ganglion. The brain is continued round the oral cavity as a thick nerve-ring, the ventral part of which forms the sub-oesophageal ganglion, united by two longitudinal commissures to the first ventral ganglion. Thus the brain has two channels of communication between it and the ventral nerve-cord on each side, one by means of the slender nerve above mentioned, and one through the sub-oesophageal ganglion. The ventral chain is composed of four ganglia connected together by widely divaricated commissures. Each ganglion gives off three pairs of nerves, two to the ventral musculature, and one to the dorsal. The terminations of these nerves in the muscles are very clearly seen in these transparent little creatures, though there is still much dispute as to their exact nature.

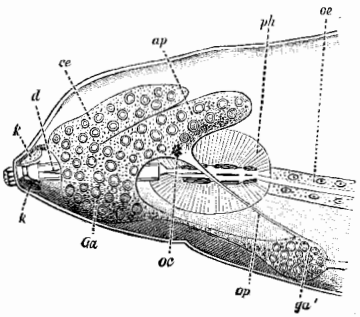

FIG. 253.—Brain of *Macrobiotus hufelandi*, C. Sch., × about 350. (From Plate.) Seen from the side. *ap*, Lobe of brain bearing the eye; *ce*, supra-oesophageal ganglion; *d*, tooth; *Ga*, first ventral ganglion; *ga'*, sub-oesophageal ganglion; *k*, thickening of the epidermis round the mouth; *oc*, eye-spot; *oe*, oesophagus; *op*, nerve running from the ocular lobe of the brain to the first ventral ganglion; *ph*, pharynx.

The older writers considered the Tardigrada as hermaphrodites, but Plate and others have conclusively shown that they are bisexual, at any rate in the genus *Macrobiotus*. The males are, however, much rarer than the females. The reproductive organs of both sexes are alike. Both ovary and testis are unpaired structures opening into the intestine, and each is provided with a dorsal accessory gland placed near its orifice. In the ovary many of the eggs are not destined to be fertilised, but serve as nourishment for the more successful ova which survive.

No special circulatory or respiratory organs exist, and, as in many other simple organisms, there is no connective tissue.

The segmentation of the egg in *M. macronyx* is total and equal, according to the observations of von Erlanger.[1] A blastula, followed by a gastrula, is formed. The blastopore closes, but later the anus appears at the same spot. There are four pairs of mesodermic diverticula which give rise to the coelom and the chief muscles. The reproductive organs arise as an unpaired diverticulum of the alimentary canal, which also gives origin to the Malpighian tubules. The development is thus very primitive and simple, and affords no evidence of degeneration.

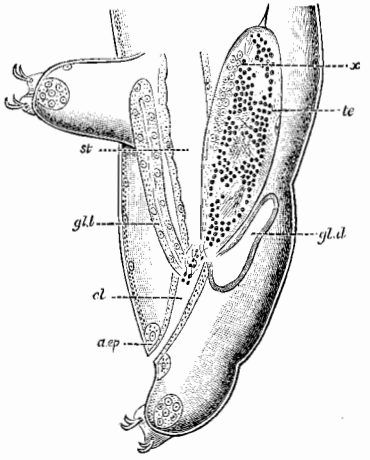

FIG. 254.—Male reproductive organs of *Macrobiotus hufelandi*, C. Sch., × about 350. (From Plate.) *a.ep*, Epidermal thickening round anus; *cl*, cloaca; *gl.d*, accessory gland; *gl.l*, Malpighian gland; *st*, stomach; *te*, testis; *x*, mother-cells of spermatozoa.

With regard to their position in the animal kingdom, writers on the Tardigrada are by no means agreed. O. F. Müller placed them with the Mites; Schultze and Ehrenberg near the Crustacea; Dujardin and Doyère with the Rotifers near the Annelids; and von Graff with the Myzostomidae and the Pentastomida. Plate regards them as the lowest of all air-breathing Arthropods, but he carefully guards himself against the view that they retain the structure of the original Tracheates from which later forms have been derived. He looks upon Tardigrades as a side twig of the great Tracheate branch, but a twig which arises nearer the base of the branch than any other existing forms. These animals seem certainly to belong to the Arthropod phylum, inasmuch as they are segmented, have feet ending in claws, Malpighian tubules, and an entire absence of cilia. The second and third of these features indicate a relationship with the Tracheate groups; on the other hand there is an absence of paired sensory appendages, and of mouth-parts. Von Erlanger has pointed out that the Malpighian tubules, arising as they do from the mid-gut, are not homologous with the Malpighian tubules of most Tracheates,

[1] *Morph. Jahrb.* xxii., 1895, p. 491.

and he is inclined to place this group at the base or near the base of the whole Arthropod phylum. They, however, show little resemblance to any of the more primitive Crustacea. The matter must remain to a large extent a matter of opinion, but there can be no doubt that the Tardigrades show more marked affinities to the Arthropods than to any other group of the animal kingdom.

Biology.—Spallanzani, who published in the year 1776 his *Opuscules de physique animale et végétale*, was the first satisfactorily to describe the phenomena of the desiccation of Tardigrades, though the subject of the desiccation of Rotifers, Nematodes, and Infusoria had attracted much notice, since Leeuwenhoek had first drawn attention to it at the very beginning of the century. In its natural state and in a damp atmosphere Tardigrades live and move and have their being like other animals, but if the surroundings dry up, or if one be isolated on a microscopic slide and slowly allowed to dry, its movements cease, its body shrinks, its skin becomes wrinkled, and at length it takes on the appearance of a much weathered grain of sand in which no parts are distinguishable. In this state, in which it may remain for years, its only vital action must be respiration, and this must be reduced to a minimum. When water is added it slowly revives, the body swells, fills out, the legs project, and gradually it assumes its former plump appearance. For a time it remains still, and is then in a very favourable condition for observation, but soon it begins to move and resumes its ordinary life which has been so curiously interrupted.

All Tardigrades have not this peculiar power of revivification—anabiosis, Preyer calls it—it is confined to those species which live amongst moss, and the process of desiccation must be slow and, according to Lance,[1] the animal must be protected as much as possible from direct contact with the air.

According to Plate, the Tardigrada are free from parasitic Metazoa, which indeed could hardly find room in their minute bodies. They are, however, freely attacked by Bacteria and other lowly vegetable organisms, and these seem to flourish in the blood without apparently producing any deleterious effects on the host. Plate also records the occurrence of certain enigmatical spherical bodies which were found in the blood or more usually in the cells

[1] *C. R. Ac. Sci.* cxviii., 1894, p. 817.

of the stomach. These bodies generally appeared when the Tardigrades were kept in the same unchanged water for some weeks. Nothing certain is known as to their nature or origin.

Systematic.—A good deal of work has recently been done by Mr. James Murray on the Polar Tardigrades and on the Tardigrades of Scotland, many of which have been collected by the staff of the Lake Survey.[1] Over forty species have been described from North Britain.

The following table of Classification is based on that drawn up by Plate:—

Table of Genera.

I. The claws of the legs are simple, without a second hook. If there are several on the same foot they are alike in structure and size.
  A. The legs are short and broad, each with at least two claws.
    2–4 claws . . . Gen. 1. *ECHINISCUS*, C. Sch. (Fig. 249).
    7–9 claws . . Sub-gen. 1*a*. *ECHINISCOIDES*, Plate.
  B. The legs are long and slender; each bears only one small claw. Gen. 2. *LYDELLA*, Doy.

II. The claws of the legs are all or partly two- or three-hooked. Frequently they are of different lengths.
  A. There are no processes or palps around the mouth.
    I. The muscular sucking pharynx follows closely on the mouth-tube.
      α. The oral armature consists on each side of a stout tooth and a transversely placed support. Gen. 3. *MACROBIOTUS*, C. Sch. (Fig. 252).
      β. The oral armature consists on each side of a stylet-like tooth without support. Gen. 4. *DOYERIA*, Plate.
    II. The mouth-tube is separated from the muscular sucking pharynx by a short oesophagus. Gen. 5. *DIPHASCON*, Plate (Fig. 255).
  B. Six short processes or palps surround the mouth, and two others are placed a little farther back. Gen. 6. *MILNESIUM*, Doy.

1. Genus *ECHINISCUS* (= *EURYDIUM*, Doy.).—The dorsal cuticle is thick, and divided into a varying number of shields, which bear thread- or spike-like projections. The anterior end forms a proboscis-like extension of the body. Two red eye-spots. There are many species, and the number has increased so rapidly in the last few years that specialists are talking of splitting up the

[1] *Tr. R. Soc. Edinb.* xlv., 1908, p. 641. This contains a Bibliography of recent literature. See also Richters, *Zool. Anz.* xxx., 1906, p. 125, and Heinis, *Zool. Anz.* xxxiii., 1908, p. 69.

genus. *E. arctomys*, Ehrb.; *E. mutabilis*, Murray; *E. islandicus*, Richters; *E. gladiator*, Murray; *E. wendti*, Richters; *E. reticulatus*, Murray; *E. oihonnae*, Richters; *E. granulatus*, Doy.; *E. spitzbergensis*, Scourfield;[1] *E. quadrispinosus*, Richters; and *E. muscicola*, Plate, are all British. More than one-half of these species are also Arctic, and *E. arctomys* is in addition Antarctic. In fact, the group is a very cosmopolitan one. The genus is also widely distributed vertically, specimens being found in cities on the sea level and on mountains up to a height of over 11,000 feet.

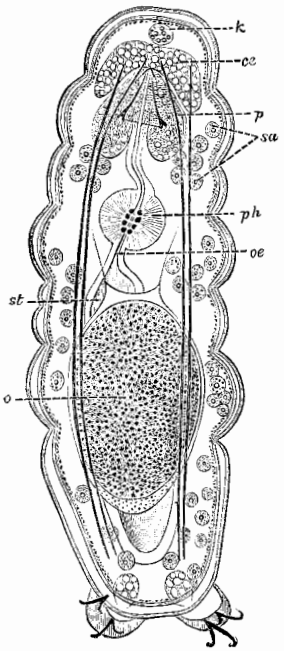

FIG. 255.—*Diphascon chilenense*, Plate, × about 100. (From Plate.) *ce*, Brain; *k*, thickening of the epidermis above the mouth; *o*, egg; *oe*, oesophagus; *p*, ? salivary glands; *ph*, pharynx; *sa*, blood corpuscles; *st*, stomach.

1*a*. Sub-genus *ECHINISCOIDES* differs from the preceding in the number of the claws, the want of definition in the dorsal plates, and in being marine. The single species *E. sigismundi*, M. Sch., is found amongst algae in the North Sea (Ostend and Heligoland).

2. Genus *LYDELLA*.[2]—The long, thin legs of this genus have two segments, and in other respects approach the Arthropod limb. Marine. Plate suggests the name *L. dujardini* for the single species known.

3. Genus *MACROBIOTUS* has a pigmented epidermis, but eye-spots may be present or absent. The eggs are laid one at a time, or many leave the body at once. They are either quite free or enclosed in a cast-off cuticle. The genus is divided into many species and shows signs of disruption. They mostly live amongst moss: but *M. macronyx*, Doy., is said to live in fresh water. The following species are recorded from North Britain: *M. oberhäuseri*, Doy.; *M. hufelandi*, Schultze; *M. zetlandicus*, Murray: *M. intermedius*, Plate; *M. angusti*, Murray; *M. annulatus*, Murray:

[1] *P. Zool. Soc.* 1897, p. 790.

[2] Hay, in *P. Biol. Soc. Washington*, xix., 1906, p. 46, states that the name *Lydella*, Dujardin, is preoccupied, and suggests as a substitute *Microlyda*.

M. tuberculatus, Plate; *M. sattleri*, Richters; *M. papillifer*, Murray: *M. coronifer*, Richters; *M. crenulatus*, Richters; *M. harmsworthi*, Murray; *M. orcadensis*, Murray; *M. islandicus*, Richters; *M. dispar*, Murray; *M. ambiguus*, Murray; *M. pullari*, Murray; *M. hastatus*, Murray; *M. dubius*, Murray; *M. echinogenitus*, Richters; *M. ornatus*, Richters; *M. macronyx*? Doy.

4. Genus *DOYERIA*.—The teeth of this genus have no support, and the large salivary glands of the foregoing genus are absent; in other respects *Doyeria*, with the single species *Doyeria simplex*, Plate, resembles *Macrobiotus*, and is usually to be found in consort with *M. hufelandi*, C. Sch.

5. Genus *DIPHASCON* resembles *M. oberhäuseri*, Doy., but an oesophagus separates the mouth-tube from the sucking pharynx, and the oral armature is weak. The following species are British, the first named being very cosmopolitan, being found at both Poles, in Chili, Europe, and Asia: *D. chilenense*, Plate; *D. scoticum*, Murray; *D. bullatum*, Murray; *D. angustatum*, Murray; *D. oculatum*, Murray; *D. alpinum*, Murray; *D. spitzbergense*, Murray.

6. Genus *MILNESIUM* has a soft oral armature, and the teeth open straight into the mouth. A lens can usually be distinguished in the eyes. Two species have been described, *M. tardigradum*, Doy., British, and *M. alpigenum*, Ehrb. Bruce and Richters consider that these two species are identical.