The Tegumental Glands in the Land Isopoda

B. The Lobed Glands: Structure and Distribution

By H. GORVETT

(From the Department of Zoology and Applied Entomology, Imperial College of Science and Technology, London, S.W. 7)

SUMMARY

1. The structure and distribution of the lobed glands in *Porcellio scaber* Latr. are described.

2. The glands have a remarkable structure, each being deeply divided into many lobes, and provided with four nuclei which do not appear to be separated by cell membranes.

3. They open externally at intervals along the margins of the body, on the lateral plates and uropods, always by separate pores, and always in exposed positions.

4. The lateral plate and uropod glands resemble each other in many respects, but differ in size, staining reactions, and type of secretion.

5. The glands do not differ in the two sexes, and are present in young animals newly liberated from the brood pouch.

6. The glands of *Porcellio scaber* Latr. are compared with those of one species of each of the following genera: *Asellus*, *Limnoria*, *Idotea*, *Ligia*, *Ligidium*, *Trichoniscus*, *Haplophthalmus*, *Oniscus*, *Platyarthrus*, *Hemilepistus*, and *Armadillidium*.

7. Lobed glands are peculiar to the terrestrial Isopoda (Oniscoidea), and appear to be present in all genera of this group, but no related structures are known in other Crustacea.

8. They vary little in essential structure or distribution in the various genera.

9. They vary considerably in size and number, but this variation is independent of sex, moulting condition, evolutionary position, respiratory mechanism, or humidity requirement.

10. The lobed glands appear to have been evolved in adaptation to terrestrial life, but their function does not seem to be connected in any way with the problems of reproduction, moulting, respiration in air, or adaptation to dry surroundings.

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INTRODUCTION

TEGUMENTAL glands in the land Isopoda are remarkably abundant, widely distributed, and varied in structure. Five (possibly six) distinct varieties have been briefly described, and one group—the rosette glands—has been discussed at length, in a previous paper (Gorvett, 1946). The latter were shown to have the same function as similar glands in the Decapoda (Yonge, 1932), being intimately concerned with the formation of the outer layer of cuticle (which corresponds in position with the epicuticle of insects).

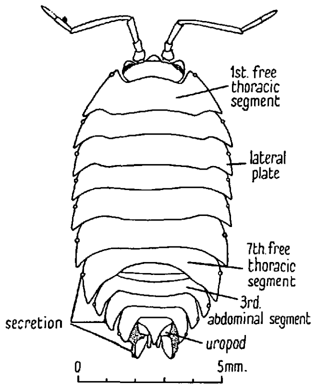

FIG. 1. Dorsal view of whole animal, showing droplets of secretion discharged by uropod glands (stippled) and lateral plate glands (unstippled). The droplets indicate the positions of the gland openings. This, and all the following figures (except fig. 11), refer to *Porcellio scaber*.

The present publication is concerned with the lobed glands, which are not only the largest, but also in many ways the most interesting of the tegumental glands in the Isopoda. They open by long ducts at the edges of the lateral plates and uropods, and appropriate stimulation (which may be accidental, as during fixation) induces them to discharge a series of clearly visible droplets (fig. 1), of which some have a pungent odour and others can be drawn out into long viscous threads. These peculiar secretions, together with the large size, unique appearance, and tightly packed arrangement of the lobed glands, have led to their attracting the attention of a number of workers. Their structure and distribution have been described, with varying degrees of accuracy, at intervals for the greater part of a century. Many attempts have also been made to solve the problem of function, but the arguments advanced have been unconvincing, and the evidence inconclusive or non-existent. Indeed, for structures which are so well developed, and so sharply restricted in their distribution to a compact group of genera with well-defined habits and mode of life, it has proved singularly difficult to produce more than a few shreds of circumstantial evidence in support of any of the theories advanced.

The work described here was begun some years ago, but publication was delayed in the hope of obtaining more satisfactory evidence on this point. The problem has been re-examined at infrequent intervals, and though positive evidence is still somewhat elusive, much information has been accumulated, and it seems undesirable to delay publication further. The present paper deals only with the structure and distribution of the lobed glands. An account of their secretions, and of experimental and other evidence concerning their functions, as well as descriptions of other types of tegumental gland, will be given elsewhere.

In addition to a detailed investigation of the lobed glands in one species (*Porcellio scaber* Latr.), an attempt has been made to compare the condition of the lobed glands in twelve different genera, to discover any differences that may exist in their abundance and structure, and to determine how far such differences may be correlated with the evolutionary position, habitat, and mode of life of the animals concerned. An investigation along these lines is all the more necessary in view of the paucity of evidence relating to the functions of these peculiar structures, and, in the hope of revealing clues to this problem, it has been made as complete as possible.

Previous Work

There have been two main sources of confusion in the work of previous authors. The first was the mistaken idea of 'Weber's glands'. Many writers, following Herold (1913), have distinguished between three groups of lobed glands, opening respectively on the uropods, lateral plates, and at the bases of the pleopods. It has already been shown (Gorvett, 1950) that the third group, known as 'Weber's glands', does not exist. The idea originated in 1909 (Bepler) through misinterpretation of previous work, and took root when the non-existent glands received a name in 1913 (Herold). The second source of confusion has been the failure of some previous authors to distinguish between lobed glands and other types of tegumental gland. The latter occur both in the uropods and lateral plates and in other parts of the body, though never at the bases of the pleopods.

Of the innumerable references to the lobed glands in the literature, only the more important are mentioned here. The uropod glands appear to have been discovered first. They were described in 1853 by Lereboullet, who noticed a viscous fluid escaping from the uropods of certain woodlice and compared this secretion with the silk of spiders. They were next mentioned in 1865 by Wagner, and were regarded by him as defence glands. Glands found in *Astacus* by Braun (1875), and in *Orchestia* by Nebeski (1880), were believed by Herold (1913) to be homologous with the lobed glands of the Isopoda, but this is most unlikely: the glands discovered by Braun were probably rosette glands, while the glands of *Orchestia*, though perhaps comparable with certain other types of tegumental gland in the Isopoda, have little in common with the lobed glands.

The lateral plate glands were first noted by Weber (1881) who was unacquainted with Wagner's work. From his examination of cleared and teased preparations, mostly of *Trichoniscus*, he wrongly concluded that the glands are confined to the hinder part of the body and always open on the under side. This misled him into assuming that the secretion serves to moisten the gills. A year later Huet (1882), without knowledge of Weber's work, found lobed glands in all segments of the body in various Oniscidae, and gave the first adequate account of the duct openings. Like Wagner, he regarded the glands as defence organs. Ide (1891) was the first to examine sectioned material, and he was able to give a detailed and accurate account of the structure of the uropod glands of *Oniscus*, but the lateral plate glands are not mentioned. He compared the secretion with the silk of Lepidoptera and spiders, but gave no opinion as to its function.

In 1895 and 1896 Němec described certain branching canals in the abdomen which he considered to be excretory organs with external openings at the bases of the pleopods. As already pointed out (Gorvett, 1950), these structures were confused by Bepler (1909) with the lobed glands incorrectly described by Weber (1881), though they are entirely unrelated to these, do not appear to open externally, and probably serve to control the flow of blood (Kimus, 1897; Unwin, 1932).

Meanwhile in 1907 Hewitt published a monograph on *Ligia* in which there is no mention of lobed glands. Also in 1907, and again in 1908, Verhoeff (who was apparently unacquainted with the works of Wagner, Huet, and Ide) gave comparative accounts of the distribution of the lobed glands in numerous genera. He believed the glands to be defensive in function and considered the arrangement of the pores to be a useful distinguishing feature in classification. As Herold (1913) pointed out, however, the pores are often very differently developed in members of the same species, and even on opposite sides of the same segment. Neither Verhoeff nor Ter-Poghossian (1909), whose description of the glands in *Porcellio* agrees closely with that of Ide for *Oniscus*, made any mention of 'Weber's glands'.

Bepler, in the paper mentioned above (1909), dealt primarily with respiration. He does not appear to have made any original observations on the lobed glands, and his interpretation of previous work was muddled. The confusion in his paper between Weber's lobed glands and Němec's 'excretory canals' was the starting-point of the 'Weber's gland' story, and his mistaken belief that the lobed glands open on the ventral surface of the abdomen helped to bolster up Weber's view that they serve to moisten the gills.

Herold, in his monumental paper of 1913, accepted Bepler's hybrid structures without question, and regarded them as a separate group of lobed glands entirely distinct from those of the uropods and lateral plates. He was responsible for giving them the name of 'Weber's glands'. He gave detailed accounts of the distribution and structure of the lobed glands in several species, dealing more especially with the lateral plate glands in the belief that 'Weber's glands' and the uropod glands had already received adequate attention from previous authors. He discussed the origin and functions of the lobed glands, and in addition to gill moistening and defence, he suggested other possible functions connected with moulting, lubrication, and nourishment of the young.

In 1921 Collinge published a 'preliminary study' of the lobed glands of *Porcellio dilatatus* Latr., but this appears never to have been amplified, apart from a brief reference in 1943, and perhaps another (relating to 'gland cells in the epidermis') in 1945. He was not acquainted with Herold's paper and made no mention of 'Weber's glands'. Mödlinger, in a paper on respiration (1931), briefly mentioned the relative development of the lobed glands in various species, but made no detailed observations. Finally, a paper on the rosette glands (Gorvett, 1946), and a short discussion on 'Weber's glands' (Gorvett, 1950), have already been noted.

Material and Methods

Little need be added to the account of methods given in the first paper in this series (Gorvett, 1946). For most purposes, 95 per cent. alcohol still appears to be the most satisfactory fixative, but immersion in cold fixatives causes the lobed glands to discharge their secretion (fig. 1), and in section they then present an empty shrunken appearance (fig. 3). Preliminary anaesthetization with chloroform and similar substances has little deterrent effect. Secretion may almost invariably be prevented, however, by rapid fixation in alcohol heated to 60° C.

Porcellio scaber Latr., in which both groups of lobed glands are well developed, was the species chosen for the main investigation, and the lobed glands were examined in sections of individuals of different sexes, ages, and moulting stages. Sections were also made of animals subjected to a variety of treatments, but these will be more fully described in the account of the experimental work. Lateral plates and uropods were removed and mounted in glycerine or in Gurr's water-mounting medium for the examination of duct openings.

The other eleven species investigated were chosen mainly with the object of including representatives of the widest possible range of systematic position, habitat, and mode of life. With *Porcellio scaber* Latr., they comprise one species from each of twelve genera, selected from four distinct sub-orders of Isopoda (Calman, 1909), and from five widely separated families within the sub-order Oniscoidea (Verhoeff, 1938; Vandel, 1943). They include forms living in habitats ranging from sea-water and fresh water, through low and high shore levels, damp terrestrial and other intermediate conditions, to dry desert. Closely correlated with the habitat is the mode of respiration, and each of the three chief respiratory modifications is present in one or more of the species examined (Stoller, 1899; Verhoeff, 1919; Unwin, 1932; &c.). These modifications, which affect the pleopod exopodites only, include (1) decrease in thickness of the epidermis and cuticle of the whole of the exposed ventral surface (Stoller's version of this is incorrect); (2) development of thin-walled border organs which entrap bubbles of air (Unwin denied the existence of the internal air cavities described by Stoller and others); (3) development of tree-like 'pseudotracheae'. A list of the species investigated is given in Table 1, together with the systematic position, the habitat, and the respiratory modification of the pleopod exopodites, of each one.

TABLE 1

Sub-order	*Family*	*Species*	*Habitat*	*Respiratory mechanism*
Asellota	Asellidae	*Asellus aquaticus* Linn.	Fresh water	Gill
Flabellifera	Limnoriinae	*Limnoria lignorum* Rathke	Sea-water	,,
Valvifera	Idoteidae	*Idotea granulosa* Rathke	Low shore	Gill covered by operculum
Oniscoidea	Ligiidae	*Ligia oceanica* Linn.	High shore	Thin ventral wall
,,	,,	*Ligidium hypnorum* Cuv.	Very damp terrestrial	,,
,,	Trichoniscidae	*Trichoniscus pusillus* Brdt.	Damp terrestrial	,,
,,	,,	*Haplophthalmus danicus* B.-L.	Damp terrestrial	,,
,,	Oniscidae	*Oniscus asellus* Linn.	Less damp terrestrial	Thin-walled border organ
,,	Porcellionidae	*Platyarthrus hoffmannseggii* Brdt.	Ants' nests	Thin ventral wall
,,	,,	*Porcellio scaber* Latr.	Fairly dry terrestrial	Two pairs pseudotracheae
,,	,,	*Hemilepistus klugii* Brdt.	Desert	Three pairs pseudotracheae
,,	Armadillidiidae	*Armadillidium vulgare* Latr.	Dry terrestrial	Two pairs pseudotracheae

The specimens of *Hemilepistus klugii* Brdt. were found in particularly arid conditions in the desert in Cyrenaica, and were kindly supplied by the late Professor H. G. Jackson. *Ligidium hypnorum* Cuv. was obtained through the kindness of Dr. Isabella Gordon. This list is referred to below as an 'evolutionary series'. This alludes only to the increasing specialization of the various species (particularly in adaptation to habitat, and methods of respiration), and though representing their probable relative position in the hierarchy of the group according to the latest views (Vandel, 1943), it does not imply direct continuity of evolution.

OBSERVATIONS

Structure in Porcellio scaber

Though the lateral plate and uropod glands form secretions which differ in several important respects (notably pH, viscosity, and odour), they closely resemble each other in structure. Indeed, the lobed glands of widely separated genera appear to differ from one another only in details. The lobed glands of *Porcellio scaber* Latr. may therefore be regarded as typical, and the description of these which follows differs little from Ide's account of the uropod glands of *Oniscus asellus* Linn.

Each of the lobed glands (figs. 2 and 3) consists of a large mass of cytoplasm and a conspicuous, often elongated, duct. These glands should perhaps be

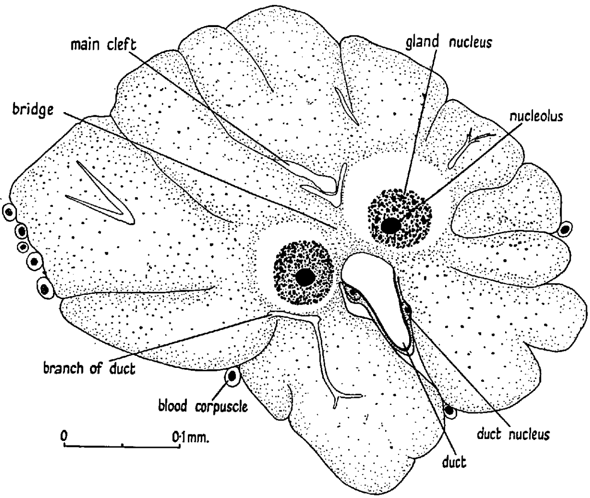

FIG. 2. Section through the middle of a uropod gland which has not discharged its secretion. This section shows the main cleft almost completely dividing the gland into two parts, and the narrow connecting bridge of cytoplasm.

termed non-cellular since each is provided with two large nuclei (which contain conspicuous nucleoli) embedded in the gland cytoplasm, and two additional smaller nuclei in the wall of the duct. No trace of cell membranes separating these can be detected. The gland cytoplasm is more or less spherical in shape, but often distorted by the pressure of surrounding glands or other tissues. Undischarged glands frequently reach a diameter of 0·5 mm. in section. The gland is deeply divided into two more or less equal parts joined by only a narrow bridge of cytoplasm (fig. 2). Each part is subdivided into a number of lobes by fissures which, in fully developed glands, extend half-way or more towards the centre of the gland. In undischarged glands the lobes are in close contact, leaving little space between them. In young glands these divisions are less well marked.

The cytoplasm has a granular appearance in section, or shows a fine network. It is stained lightly with acid stains, and appears to be homogeneous, except that it is less dense in texture, and tends to take up less stain, in the middle of each lobe (presumably owing to the presence here of unstained secretory material). The large vacuoles mentioned and figured by Ide have rarely been seen, and then only in poorly fixed material; they appear to be artifacts.

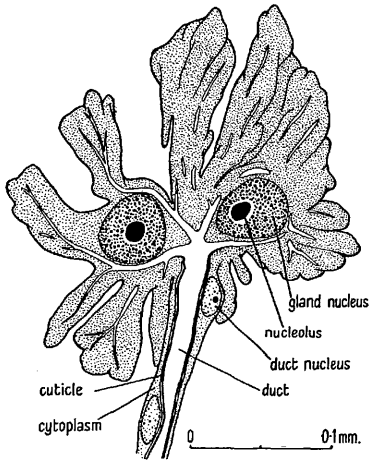

FIG. 3. Section through the middle of a uropod gland which discharged its secretion during fixation. This gland is from the same part of the body, and from an animal of approximately the same age and size, as the gland shown in fig. 2.

As mentioned above, the glands readily discharge when fixed in cold solutions, and in sections of animals so treated the glands (fig. 3) present an appearance very different from that of undischarged glands (fig. 2). The glands shown in figs. 2 and 3 occupied the same part of the uropod in similar animals, and differ only in that the first discharged its secretion during fixation, the second did not. In the discharged gland, the lobes have a shrunken appearance; they are much shorter and more widely separated. The gland as a whole is thus considerably reduced in size, and the spaces between the lobes are much enlarged. The difference is very noticeable in sections of the whole uropod, in which undischarged glands almost completely fill the entire cavity (fig. 5). The cytoplasm of discharged glands is more dense in texture and more deeply stained, but otherwise differs little in appearance from that of undischarged glands.

The ducts are very conspicuous (fig. 3), and each has a large lumen. The duct enters the secretory part of the gland at the narrow bridge connecting the two halves, and immediately divides into a number of branches which pass round the nuclei and ramify through the cytoplasm. Two nuclei are always present on the duct, near its point of entry into the secretory mass; they lie embedded in the wall, at a short distance apart, and on opposite sides. Even in the longest ducts, no other nuclei can be found. The wall of the duct is stained blue with Mallory. The thin layer of cytoplasm which surrounds the duct nuclei appears to be continued over the surface of the duct wall and to form the greater part of its thickness. This appears to be lined with a thin layer of chitin, and in some sections it is possible to detect an excessively thin inner lining of material which is stained red with Mallory and which may correspond with the outer cuticle layer ('epicuticle') of the integument. The ducts never join: each invariably opens to the outside by a separate pore (figs. 7, 8, and 10). The lumen enlarges slightly in its passage through the chitinous layer of the integument to form a small ampulla (figs. 8 and 10). This projects very slightly from the surface as a minute rim, and the actual opening is smaller in diameter than the rest of the duct.

The glands of both groups lie freely in the haemocoele, or surrounded by a loose connective tissue containing abundant blood spaces (fig. 8). Blood corpuscles can often be seen between the lobes (fig. 2), and the cytoplasm of the gland is clearly in close contact with the blood. The peculiar lobed structure thus has the effect of greatly increasing the surface area of protoplasm in contact with the blood. This may, perhaps, be of importance to an active organ which has no efficient capillary blood-system, and there is no evidence that the lobing serves any other purpose.

Both the glands and their external pores vary in size, and small glands, apparently not yet fully developed, can often be found among the normal glands in both uropods and lateral plates (fig. 4). They appear, from the fine texture and deeper staining of their cytoplasm, to be immature rather than small mature forms. Even those with a diameter of only 0·05 mm. (less than one-tenth that of the largest glands) already possess, like the glands of newly liberated young, the normal four-nucleated structure and the main cleft into two parts, though the lobing is less well marked. The lobed glands presumably develop as ingrowths from the epidermis, but it is uncertain whether each gland is originally derived from one, two, or four, distinct epidermal cells. No evidence has been found in support of Herold's suggestion that the four-nucleated glands may arise by fusion of two separate two-nucleated glands.

There are never any traces of degenerating glands (in contrast to discharged glands), such as are to be found at certain stages of the moulting cycle in the case of the rosette glands. Unlike the latter, the lobed glands appear to be capable of repeated discharges of secretion, for it is possible (though by no means easy) to stimulate an animal to discharge its lobed glands without killing it, and to bring about second and further discharges after sufficient periods of recovery. The time interval of several hours required between successive discharges would appear to be sufficient for the replenishing of secretory material in the existing glands, but much too short for the development of an entirely new set of glands. The possibility that the lobed glands may play some part in the moulting process will be discussed more fully in the account of the experimental work.

Distribution in Porcellio scaber

It has already been pointed out that Herold's division of the lobed glands into three groups is incorrect, and that all lobed glands open either on the uropods or on the lateral plates. The uropod glands in *Porcellio scaber* are large (up to 0·5 mm. in diameter in section), very numerous (between fifty and sixty on each side of the body), and occupy the cavities of the protopodite

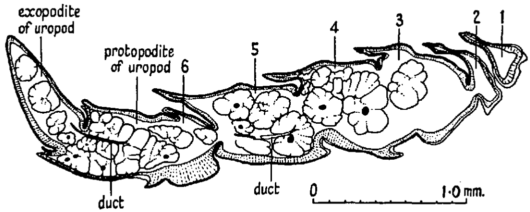

FIG. 4. Section through abdomen and uropod, showing the complete range of distribution of the uropod glands. The section was cut at a slight angle to the longitudinal axis, diverging outwards from the mid-line anteriorly. The figures refer to the abdominal segments.

and exopodite of the uropod, and of the third, fourth, and fifth abdominal segments (fig. 4). The first and second abdominal segments are reduced in *Porcellio*, as in most genera; they have no lateral plates, and usually contain no lobed glands of either group. The glands almost completely fill the cavities of the structures which they occupy, leaving little room even for the blood (fig. 5). In the abdomen they lie on each side of the rectum, extending into the bases of the lateral plates so as to lie alongside the lateral plate glands (fig. 6). The ducts from all the uropod glands pass backwards into the bases of the uropods, and open (without anastomosing) on their lateral edges (figs. 1 and 7). The ducts from the more anterior glands open on the protopodite at the base of a broad groove on its outer surface. Ducts from the remaining glands open in a row along the outer edge of the single segment of the exopodite, in a slight groove below a projecting ridge.

Lateral plate glands occur in each of the seven free thoracic segments, and in the third, fourth, and fifth segments of the abdomen (fig. 1). They are rather smaller than the uropod glands (not more than 0·2 mm. in diameter), and have even less affinity for acid stains (which is not surprising in view of the strongly acid reaction of the secretion they produce). They lie in a fairly compact group towards the base of each plate, and the ducts from all the glands in the group converge (without actually joining) to open into a restricted pore area on the distal edge of the outer (dorsal) surface of the plate (fig. 8). The pore area lies on a narrow rim that runs round the edge of the plate (fig. 9). This

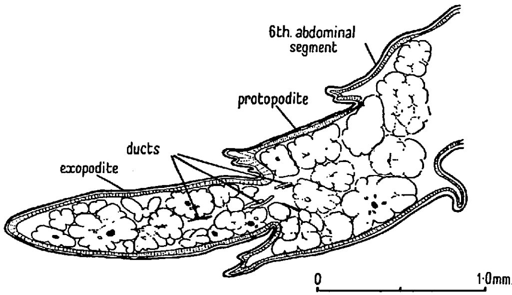

FIG. 5. Longitudinal section of uropod, showing the uropod glands almost completely filling the internal cavity.

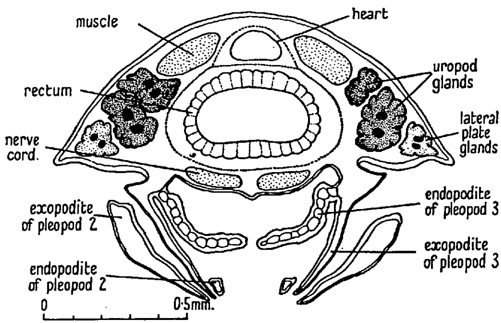

FIG. 6. Transverse section of the third abdominal segment, showing the uropod glands and lateral plate glands lying side by side at the bases of the lateral plates on each side of the rectum.

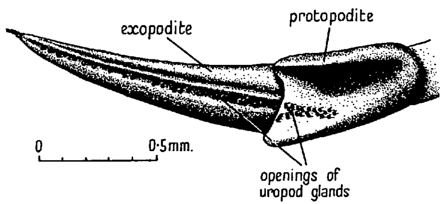

FIG. 7. Side view of the outer edge of the right uropod, showing the openings of the uropod glands.

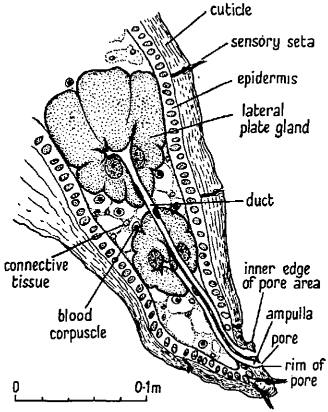

FIG. 8. Transverse section of lateral plate of thoracic segment, showing two lateral plate glands and their ducts.

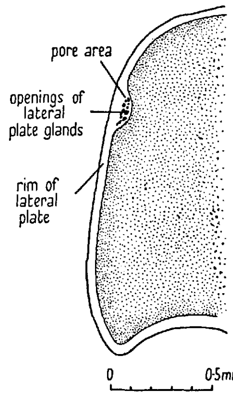

FIG. 9. View of outer (dorsal) surface of the lateral plate of the second thoracic segment, showing the pore area into which the ducts of the lateral plate glands open.

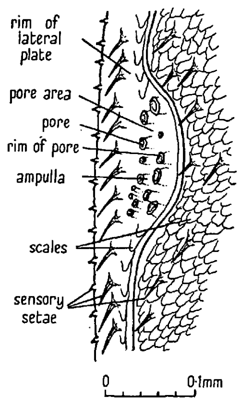

FIG. 10. View of the pore area shown in fig. 9 under higher magnification, showing the duct openings with their minute projecting rims. Parts of the ampulla-like endings of the ducts can also be seen lying in the thickness of the transparent cuticle.

rim is almost devoid of the scales that overlie the cuticle elsewhere, though well provided with sensory setae; at the pore area it widens out and loses both scales and setae (fig. 10). The pore area on each segment lies just behind the backwardly projecting tip of the lateral plate in front (fig. 1). It is situated towards the front of the plate in the anterior segments, slightly farther back in each successive segment, until in the abdomen it lies nearer the hinder edge of the plate.

The number of glands in each plate (most easily determined by counting the pores) is very variable, and often differs, as Herold pointed out, on opposite sides of the same segment. The figures obtained (slightly higher than those given by Herold) vary from about 14 to 21 for the thoracic segments (Herold gave from 8 to 20), and from 2 to 8 for the abdominal segments (Herold's figures were from 2 to 7). They may vary, perhaps, in different local populations.

There appears to be no significant difference in the numbers or appearance of the glands in the two sexes, or in individuals of different ages. In young animals newly liberated from the brood pouch, lobed glands with the normal four-nucleated structure are already present in both uropods and lateral plates. They are smaller and rather less numerous than in the adult, however, and the glands appear to increase in size and number as the animal develops.

Structure and Distribution in Other Genera

An attempt has been made to compare the lobed glands in *Porcellio scaber* with those of eleven other species. General impressions of the appearance of the glands are inadequate for this purpose unless supplemented by precise counts and measurements. The numbers of glands have been determined, wherever possible, by counting the external pores, otherwise by examination of serial sections. Though the size of the glands varies to some extent in any particular group, the majority of glands seem to be fully developed and roughly equal in size, and the maximum diameter of the largest gland in each group (measured by means of an eyepiece micrometer) has been used as a basis for comparison. In order to facilitate the comparison of the glands in the different species, the figures obtained, together with certain other observations, have been summarized in Tables 2 and 3. The diameter measurements are expressed in millimetres; the figures for the numbers of uropod glands are for one side of the body only, those for the lateral plate glands are for the average number in each thoracic lateral plate.

As indicated in the tables, the lobed glands are restricted absolutely to the sub-order Oniscoidea, i.e. to the terrestrial genera. While other types of tegumental gland are widely distributed throughout the Isopoda in both aquatic and terrestrial forms, no trace of lobed glands can be found in *Asellus*, *Limnoria*, or *Idotea*. They appear for the first time, in rudimentary form, in *Ligia*, and they are present without exception, though in varying degrees of development, in all the other genera of Oniscoidea investigated.

TABLE 2. *Uropod Glands*

Species	*Number*	*Max. diam.*	*Position of glands*	*Position of pores*	*Gland nuclei*	*Lobes*
Asellus aquaticus	None	..	..	..	..	..
Limnoria lignorum	None	..	..	..	..	..
Idotea granulosa	None	..	..	..	..	..
Ligia oceanica (mature)	None	..	..	..	..	..
Ligia oceanica (young)	1	0·04	Base of protop.	Outer wall of protop.	1 large	Few, deep
Ligidium hypnorum	5–6	0·05	Outer edge of protop.	Outer wall of protop.	1 large	Fairly numerous, deep
Trichoniscus pusillus	Over 20	0·1	Protop., exop., abd. seg. 3–6	Outer edge of protop., exop.	1 large	Many, deep
Haplophthalmus danicus	5	0·07	Protop., exop., endop.	Outer edge of protop., exop., endop.	1 medium	Few, very shallow
Oniscus asellus	Over 70	0·25	Protop., exop., abd. seg. 4–6	Outer edge of protop., exop.	2 medium	Many, deep
Platyarthrus hoffmannseggii	15–20	0·1	Protop., exop., abd. seg. 2–6	Outer edge of protop., exop.	2 small	Few, shallow
Porcellio scaber	50–60	0·5	Protop., exop., abd. seg. 3–6	Outer edge of protop., exop.	2 large	Many, deep
Hemilepistus klugii	40–50	0·4	Protop., exop., abd. seg. 3–6	Outer edge of protop., exop.	2 large	Many, deep
Armadillidium vulgare	25–30	0·27	Protop., exop., abd. seg. 4–6	Outer edge of exop. only	2 large	Fairly numerous, fairly deep

TABLE 3. *Lateral Plate Glands*

Species	*Number*	*Max. diam.*	*Position of glands*	*Pore area or ducts*	*Gland nuclei*	*Lobes*
Asellus aquaticus	None	..	..	..	..	..
Limnoria lignorum	None	..	..	..	..	..
Idotea granulosa	None	..	..	..	..	..
Ligia oceanica (mature)	None	..	..	..	..	..
Ligia oceanica (young)	3–4	0·04	Near anterior edge	None, ducts ventral	1 large	Few, deep
Ligidium hypnorum	5–6	0·05	Near outer edge	None, ducts ventral	1 large	Fairly numerous, deep
Trichoniscus pusillus	1	0·05	Near edge	None, ducts ventral	1 large	Many, deep
Haplophthalmus danicus	None	..	..	..	..	..
Oniscus asellus	14	0·1	In a group	Slightly indented	2 medium	Many, deep
Platyarthrus hoffmannseggii	1	0·05	Thoracic seg. 5, 6, 7 only	None, ducts ventral	1 large	Few, shallow
Porcellio scaber	18	0·2	In a group	Distinctly indented	2 large	Many, deep
Hemilepistus klugii	1	0·16	Near edge	None, duct dorsal	2 large	Many, deep
Armadillidium vulgare	3–4	0·14	In a group	Moderately indented	2 large	Fairly numerous, fairly deep

Ligia is peculiar in that lobed glands appear to be present only in young individuals. Examination by a variety of methods has failed completely to reveal any trace of lobed glands in any well-grown individual. Other tegumental glands, particularly the small compound variety (Gorvett, 1946), are extremely abundant in many parts of the body (including the uropods and lateral plates) in specimens of all ages, and these may have been mistaken for lobed glands by Herold (1913) and others. Lobed glands have been seen only in individuals 3 mm. long. Here, though very few in number and very small, they are typical lobed glands, clearly distinct from other types of gland. In each of the remaining genera of Oniscoidea under investigation lobed glands are present in the adult, and are presumably already present at the time of liberation from the brood pouch as noted above for *Porcellio*. In no case is it possible to detect any difference in the appearance of the glands in the two sexes.

Uropod and lateral plate glands are present together in almost all the genera examined. The only exception is *Haplophthalmus*, which has fairly well-developed uropod glands but lacks all trace of lobed glands in the lateral plates. Except in the Ligiidae, where the two varieties of gland are almost indistinguishable, the uropod glands are invariably larger than the lateral plate glands, being twice as great in diameter in *Trichoniscus*, *Platyarthrus*, and *Armadillidium*, and two and a half times in *Oniscus*, *Porcellio*, and *Hemilepistus*. In most genera they also differ from the lateral plate glands in staining reaction, as noted for *Porcellio*. In the case of other generically variable features such as general form, lobing, number and size of nuclei, the lobed glands of the uropods and lateral plates of the same animal usually resemble each other much more closely. *Platyarthrus* is exceptional in having two small nuclei in each uropod gland, but only a single large nucleus in the lateral plate gland.

The number of lobed glands varies enormously in the different genera. In the case of the uropod glands it is lowest in *Ligia*, which has only one gland in each uropod (none in the adult); it increases fairly steadily through the evolutionary series to a maximum in *Oniscus*, with over seventy glands on each side of the body; it then falls away again somewhat in *Porcellio*, *Hemilepistus*, and *Armadillidium*. The number of lateral plate glands shows no such regular rise and fall, and appears to vary independently of that of the uropod glands. Lateral plate glands are absent altogether in adult *Ligia* and in *Haplophthalmus*, while *Trichoniscus*, *Platyarthrus*, and *Hemilepistus* have a single gland in each thoracic lateral plate (in only three segments in *Platyarthrus*), and young *Ligia*, *Ligidium*, and *Armadillidium* each have between three and six glands per plate. The number is much greater in *Oniscus* with an average of fourteen, and reaches a maximum in *Porcellio* with an average of eighteen glands in each plate.

Size is another variable feature of the lobed glands, particularly in the case of the uropod glands. It is to some extent related to the size of the whole animal, small forms (both individuals and species) tending to have smaller glands than large forms; but the correlation is by no means a close one as may be seen from Table 4. Indeed the size of both types of gland seems to vary in much the same way as the number of uropod glands, increasing through the evolutionary series to a maximum (in this case in *Porcellio* instead of in *Oniscus*), then falling again (in *Hemilepistus* and *Armadillidium*). The smallest uropod glands (maximum diameter 0·05 mm.) are found in the Ligiidae;

the largest, which occur in *Porcellio*, are ten times greater in diameter (0·5 mm.), and therefore one thousand times greater in volume, than the smallest. The largest lateral plate glands are also found in *Porcellio*, but have a diameter (0·2 mm.) only four times greater than that of the smallest (0·05 mm.) which occur in the Ligiidae, *Trichoniscus*, and *Platyarthrus*.

The lobed glands of *Porcellio* have four nuclei, two large gland nuclei, and two smaller duct nuclei, an invariable arrangement whatever the size of the gland or the length of the duct. In the case of the duct nuclei, the number seems to be constant in other genera also, and two are present even in *Ligidium* with its small glands and short ducts. The presence of two gland nuclei, however, is characteristic only of the more advanced genera, and in the Ligiidae, Trichoniscidae, and in the lateral plate glands of *Platyarthrus*, there is only a single gland nucleus. These differences are not surprising in view of the great variation in gland volume. The fact that the number of nuclei is not further increased in the larger glands is probably explained by the variation in size of the nuclei themselves, the size of the nucleus being usually proportional to the size of the gland. There are certain exceptions, however, notably the nuclei of all the lobed glands of *Oniscus* and of the uropod glands of *Haplophthalmus* which are relatively small, and the uropod gland nuclei of *Platyarthrus* which are relatively very small in proportion to the gland.

The lobed glands of *Oniscus*, *Hemilepistus*, and *Trichoniscus* are deeply divided into many lobes in much the same way as in *Porcellio*. In *Armadillidium* the divisions are fewer and less deep. In the Ligiidae (especially in *Ligia*) the number of lobes is still smaller, though in these primitive forms the gland is already deeply incised. Lobing is least well developed in the glands of *Platyarthrus* and *Haplophthalmus*, where the lobes are almost non-existent, the glands appearing rounded or polygonal in section with only a few slight indentations at the margin.

The general arrangement of the glands and the position of the duct openings is the same in all genera, though there are certain differences in detail. Naturally the amount of space occupied will vary with the number and size of the glands. In the Ligiidae, for example, the uropod glands, which are very small and very few in number, are confined to the protopodite of the uropod. In *Haplophthalmus* they spread from the protopodite into both exopodite and endopodite. In all other genera the glands not only occupy both the protopodite and exopodite of the uropod (never the endopodite), but they extend forwards into the abdomen as far as the front of segment four (*Oniscus*, *Armadillidium*), three (*Trichoniscus*, *Porcellio*, *Hemilepistus*), or even two (*Platyarthrus*). In *Platyarthrus* the glands lie in a row in the uropod and have a diameter equal to the whole width of the cavity, which they fill almost completely; they extend forwards into segment three as in other forms, and segment two is occupied by two or three smaller glands lying above the gut. The ducts from the latter are directed backwards into the uropod in the usual way. Indeed, the ducts of all lobed glands situated in the uropods and abdominal segments, however far forwards, invariably pass back into the uropods, where they open by separate pores along the outer margin. In most genera the pores extend in a series along the outer edges of both protopodite and exopodite. In the Ligiidae the ducts pass straight across to the outer wall of the protopodite, while in *Armadillidium* the ducts all open at the edge of the flattened exopodite.

The lateral plate glands, being usually smaller and less numerous than the uropod glands, show less tendency to spread. They lie singly (*Trichoniscus*, *Platyarthrus*), or in a short row (Ligiidae), near the edge of the plate, usually at the anterior corner; or where more numerous (*Oniscus*, *Porcellio*, *Armadillidium*) they form a compact group nearer the middle of the plate, but still at no great distance from the edge (as described and figured for *Porcellio*). *Trichoniscus* is unusual in having lateral plates on the first two abdominal segments, but these do not appear to contain lobed glands. This may be because lateral plates are absent in these segments in other genera. On the other hand, it may be an example of the general tendency (especially well marked in *Armadillidium* described below) for the glands to open only where they will not be hidden by the lateral plates of other segments; for the lateral plates of the first two abdominal segments in *Trichoniscus* are largely hidden below a great backward prolongation of the lateral plate of the seventh thoracic segment.

In *Oniscus* and *Armadillidium* the ducts from the glands of each group open dorsally in a pore area at the edge of the plate as in *Porcellio*, though the pore area is less deeply indented in these forms. The duct from the single gland of *Hemilepistus* opens in a similar position, but no trace of an indented pore area is visible. In *Armadillidium vulgare*, the only form investigated capable of rolling into a ball, there may be some functional significance in the fact that the gland openings are never covered over even when the animal rolls itself up (fig. 11). In the first thoracic segment there are six glands in each lateral plate instead of the usual three or four (Herold records an even more striking difference for *A. nasutum* B.L.). This would seem to be a compensation for the position of the pore area, which lies at the extreme anterior corner of the plate, separated from the pore area on the next segment by the whole length of the unusually long lateral plate of the first segment. The remaining pore areas are closer together and each one lies immediately behind the posterior edge of the plate of the segment in front. When the animal rolls itself up, the various plates swing round without covering over any of the pore areas. Furthermore, the protopodite of the uropod is unusually well hidden in *Armadillidium*, and this is the only genus in which the uropod gland openings are restricted to the exopodite.

Trichoniscus, *Platyarthrus*, and the Ligiidae have no pore areas, and each duct leaves the gland on the inner (ventral) side, and passes along in close proximity to the ventral epidermis towards the edge of the plate. The ducts are extremely slender in these forms and it is difficult to determine the exact point of penetration of the cuticle, but the duct appears to open on the inner (ventral) side of the plate at a short distance from the distal edge. The tement previously made in discussing Weber's theory of the function of the lobed glands (Gorvett, 1950) that the ducts 'invariably open on the *upper* (dorsal) surface of the lateral plate' may thus need some qualification. This does not affect the main argument, however, and, in any case, the arrangement is found only in forms which have very few, very small glands, and these cannot conceivably be capable of performing the function attributed to them by Weber. The evidence for this view will be discussed more fully elsewhere.

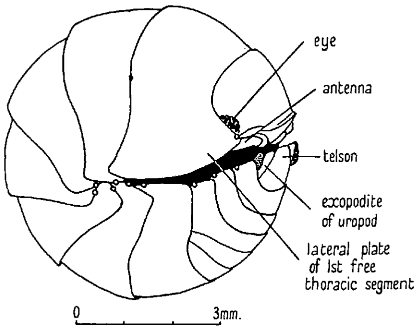

FIG. 11. Side view of *Armadillidium vulgare* which has rolled itself up and discharged its uropod and lateral plate glands. The droplets of secretion indicate the positions of the gland openings, which are never covered by the overlapping plates. The uropod gland secretion is stippled, the lateral plate gland secretion unstippled.

DISCUSSION

Before discussing the results of this investigation, it seems desirable to simplify comparison of the glands in different species by making certain corrections in the figures given in Tables 2 and 3. Since the size of the glands in *Porcellio* varies with, and is roughly proportional to, the size of the individual, and since mature individuals of different species vary very considerably in size (from 3 mm. in *Platyarthrus* to over 30 mm. in *Ligia*), it seems reasonable to assume that differences in size of the glands in different species will be at least partly due to differences in the size of the mature animals, as well as to variations in the age and size of the particular individual examined. In comparing the various species, gland size will thus have little significance unless it is related to the size of the animal, and a very approximate correction may be made by calculating the relative size of the gland (assuming it to be increased proportionally) when the length of the animal is increased in each case to a standard 100 mm. Furthermore, since the size and the number of the glands in the different species vary independently of each other, neither, taken alone, will give any real indication of the comparative development of the glands, and it is only by multiplying the two together that a satisfactory basis for comparison can be obtained. The results of these calculations have been summarized in Table 4. Column 1 shows the length of the animal in millimetres from head to telson inclusive; columns 4 and 9 the relative size of the uropod and lateral plate glands respectively calculated for an animal of standard length 100 mm.; and columns 5 and 10 the product of number and relative size. It is this final figure that may be taken as a very rough measure of the *relative* amount of glandular material in the various species. The variation is in reality even greater than indicated; for the figures given are based only on differences in gland radius, whereas the volume of gland substance (assuming the glands to be approximately spherical) is a function of the cube of the radius. In columns 6 and 11 the various species are numbered in accordance with the relative development of their glands.

TABLE 4. *Relative Development of Uropod and Lateral Plate Glands*

		Uropod glands					*Lateral plate glands*				
Species	*Length of animal*	*Number per uropod*	*Max. diam.*	*Diam. in animal 100 mm. long*	*No. times diam.*	*Order in list*	*Number per plate*	*Max. diam.*	*Diam. in animal 100 mm. long*	*No. times diam.*	*Order in list*
Ligia oceanica	3·0	1	0·04	1·3	1·3	9	3·4	0·04	1·3	5·2	4
Ligidium hypnorum	7·0	5–6	0·05	0·7	4·2	8	5–6	0·05	0·7	4·2	5
Trichoniscus pusillus	2·5	20	0·1	4·0	80·0	5	1	0·05	2·0	2·0	6
Haplophthalmus danicus	3·0	5	0·7	2·3	11·5	7	0	..	..	0	9
Oniscus asellus	12·0	70	0·25	2·1	147·0	2	14	0·1	0·8	11·2	2
Platyarthrus hoffmannseggii	3·0	15–20	0·1	3·3	66·0	6	1	0·05	1·7	1·7	7
Porcellio scaber	12·0	50–60	0·5	4·2	252·0	1	18	0·2	1·7	30·6	1
Hemilepistus klugii	17·0	40–50	0·4	2·4	120·0	3	1	0·16	0·9	0·9	8
Armadillidium vulgare	9·0	25–30	0·27	3·0	90·0	4	3–4	0·14	1·6	6·4	3

Comparison of the figures in Table 4 shows that it is in *Porcellio* that the lobed glands reach their highest level of development. If the figures in columns 5 and 10 are valid, this genus possesses almost twice as much glandular material as *Oniscus* in the case of the uropod glands, and nearly three times as much in the case of the lateral plate glands. *Oniscus* is followed fairly closely by *Armadillidium*, but while *Hemilepistus*, *Trichoniscus*, and *Platyarthrus* are also comparatively well supplied with uropod glands, the lateral plate glands in these genera are very poorly developed. In *Haplophthalmus* the uropod glands are considerably less abundant, and the lateral plate glands non-existent. The Ligiidae have the most poorly developed uropod glands, but appear to be rather better equipped with lateral plate glands than *Trichoniscus*, *Haplophthalmus*, *Platyarthrus*, and *Hemilepistus* (except in the case of adult *Ligia*, which seems to have lost completely both types of gland).

The comparative anatomy of the lobed glands has now been surveyed in some detail, and a stage has been reached at which it will be possible to make ..tain generalizations and to draw certain conclusions.

1. The lobed glands are peculiar to the terrestrial Isopoda, or Oniscoidea, and they are present in all the genera of that sub-order so far investigated. This distribution suggests that the lobed glands have evolved in adaptation to terrestrial life, and that their function may be connected in some way with the problem of living on dry land.

2. Though typical lobed glands are present in the Ligiidae, which lie near the base of the main evolutionary series of living Oniscoidea (Vandel, 1943), no structures resembling them even remotely are known in any other sub-order of Isopoda, or indeed in any other group of Crustacea. Nothing, therefore, can be said at present about their evolutionary origin.

3. The lobed glands seem to show little variation in essential structure throughout the group. The number of gland nuclei increases from one in the more primitive genera to two in the more advanced forms, but this difference is probably related to gland size rather than to evolutionary position. The peculiar lobed form of the glands may serve simply to increase the surface area in contact with the surrounding blood, but the significance of the feeble development of the gland lobing in *Haplophthalmus* and *Platyarthrus* is not obvious.

4. There seem to be no important variations in the positions of the duct openings in the different genera. These are situated at intervals along almost the whole length of the margins of the flattened body. The ducts of the uropod glands invariably open along the outer edges of the uropods; those of the lateral plate glands appear to open on the ventral side of the plates in primitive forms, in a restricted pore area on the dorsal side in more advanced genera, but always near the distal edge of the plate.

5. There may be some significance in the fact that the ducts always open separately, and also in the way in which the duct openings invariably appear to be situated in exposed positions which are never overlapped by other parts of the body. This is well seen in *Armadillidium* where both types of gland remain uncovered even when the animal rolls itself up.

6. The degree of development of the lobed glands does not differ in the two sexes or at different stages of the moulting cycle. It varies considerably in the different genera, but this variation does not appear to be correlated with the evolutionary position of the genera. Though the uropod glands show a general tendency to increase in size and abundance through the evolutionary series, they reach their maximum development in *Porcellio*, and not in the otherwise more advanced *Armadillidium*; and *Platyarthrus*, usually classed with *Porcellio* in the family Porcellionidae, takes sixth place in the matter of gland development. The condition of the lateral plate glands seems to be even more independent of the position of the genera in the hierarchy of the group.

7. The relative development of the glands in different genera does not seem to depend on the mode of respiration. The gland condition of *Armadillidium*, for instance, is closer to that of *Trichoniscus* and *Ligia* than to *Porcellio*

and *Hemilepistus*, though *Armadillidium*, *Porcellio*, and *Hemilepistus* possess pseudotracheae, *Trichoniscus* and *Ligia* do not. *Porcellio* has an abundant supply of lateral plate glands, *Hemilepistus* almost none.

8. The relative development of the glands does not seem to be correlated with the nature of the habitat. It certainly does not vary with the humidity of the surroundings, which is probably the most important single environmental factor, and which varies considerably among the different genera. *Trichoniscus* and *Haplophthalmus*, for instance, both require moist conditions, and are found, sometimes associated together, in very similar situations (e.g. among dead leaves); yet the lobed glands are very much better developed in *Trichoniscus* than in *Haplophthalmus*, both in the uropods and in the lateral plates. *Hemilepistus*, which appears to flourish in the dry desert, has its uropod glands less well developed than *Porcellio* or *Oniscus* (both of which need much damper surroundings), and has a poorer development of lateral plate glands than *Ligia* and *Ligidium* (for which the humidity requirements are greater than for any other genera).

9. It is thus apparent that comparative anatomy gives little indication of either the origin or the functions of the lobed glands. It seems very probable that their function must be linked with some feature of life on dry land, but the glands do not appear to be concerned with the problem of respiration in air, they do not seem to have evolved in adaptation to the dryness of the surroundings, and there is no evidence that they play any part in moulting or reproduction. Perhaps the most important clue is provided by the arrangement of the duct openings, but since such an arrangement would be compatible with any one of a number of possible functions, further speculation would at present be unjustified. It must be postponed until more information has been given, particularly of the properties of the secretions and of the nature of the process itself, in a later paper.

This investigation is part of a general survey of the tegumental glands of the Isopoda which was started in the Department of Zoology, University of Bristol, at the suggestion of Professor C. M. Yonge, F.R.S., and grateful acknowledgement is made of his continued interest and encouragement.

REFERENCES

Bepler, H., 1909. *Über die Atmung der Oniscoideen.* Inaug.-Diss., Greifswald (J. C. C. Bruns).

Braun, M., 1875. Arb. Inst. Würzb., **2**, 121.

Calman, W. T., 1909. *A Treatise on Zoology*, part 7, *Appendiculata*, 3rd fascicle, *Crustacea.* London (Black).

Collinge, W. E., 1921. Ann. Mag. Nat. Hist., **7**, 212.

—— 1943. Northw. Nat., **18**, 270.

—— 1945. Ann. Mag. Nat. Hist., **12**, 139.

—— 1945. Nature, **155**, 179.

Gorvett, H., 1946. Quart. J. micr. Sci., **87**, 209.

—— 1950. Nature, **166**, 115.

Herold, W., 1913. Zool. Jahrb. Jena (Anat.), **35**, 457.

Hewitt, C. G., 1907. L.M.B.C. Memoirs no. 14, *Ligia.* London (Williams & Norgate).

Huet, L., 1882. C.R. Acad. Sci. Paris, **94**, 810.

E, M., 1891. La Cellule, **7**, 345.
ᴀɪMUS, J., 1897. Ibid., **15**, 297.
LEREBOULLET, A., 1853. Mém. Soc. Nat. Hist. Strasb, **4**, 1.
MÖDLINGER, G., 1931. Stud. Zool. Budapest, **2**, 25.
NEBESKI, O., 1880. Arb. Inst. Wien, **3**, 2.
NĚMEC, B., 1895. S.B. böhm. Ges. Wiss., **45**, 1.
—— 1896. Ibid., **25**, 1.
STOLLER, J. H., 1899. Bibl. Zool., **10**, 25, 31.
TER-POGHOSSIAN, A., 1909. Z. Naturw., Stuttgart, **81**, 1.
UNWIN, E. E., 1932. Pap. Roy. Soc. Tasm., 1931, 37.
VANDEL, A., 1943. Suppl. Bull. Biol., **30**, 1.
VERHOEFF, K. W., 1907. S.B. Ges. naturf. Fr. Berl., 229.
—— 1908. Arch. Biont. Berlin, **2**, 335.
—— 1919. Zeit. wiss. Zool. Leipzig, **118**, 365.
—— 1938. Zool. Jahrb. (Syst.), **71**, 253.
WAGNER, N., 1865. Ann. Sc. nat. Zool., **4**, 317.
WEBER, M., 1881. Arch. mikr. Anat., **19**, 579.
YONGE, C. M., 1932. Proc. Roy. Soc. Lond. B, **111**, 298.