

VII.—*On the Form and Proportions of the Brain in the Oribatidæ and in some other Acarina.*

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With a Note by E. M. NELSON, F.R.M.S.

(Read 17th April, 1895.)

PLATE VI.

WHEN, some twelve years ago, I read a paper before this Society on the Anatomy of the Oribatidæ* there was one portion of the internal anatomy which was scarcely dealt with at all, namely, the brain and nervous system. That paper, however, together with the chapters on anatomy in my subsequently published 'British Oribatidæ,'† still practically contains all that is known respecting the internal anatomy of these creatures. At that time section-cutting had not attained the

EXPLANATION OF PLATE VI.

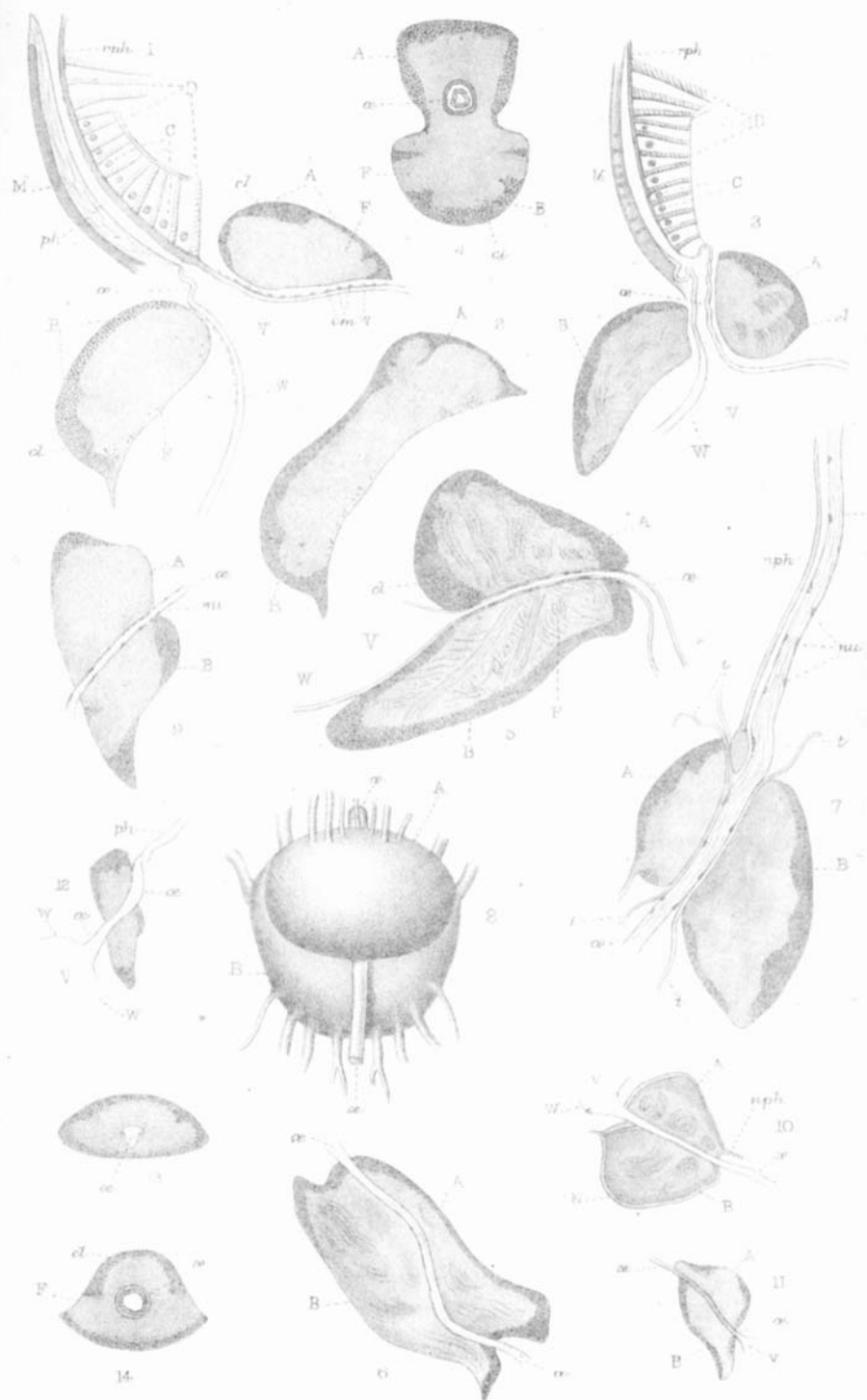
A, supra-oesophageal ganglion of the brain. B, sub-oesophageal ganglion of the brain. C, compressor muscles of pharynx cut across. *cl*, cortical layer of brain. *cm*, constrictor muscles of oesophagus. D, distensor muscles of pharynx. F, fibrous layer of brain. M, maxillary lip. N, neurilemma. *Nph*, pharyngeal nerve. *nu*, nuclei. *ph*, pharynx. *œ*, oesophagus. *rph*, roof of pharynx. *t*, tracheæ. V, ventriculus (lumen of). W, wall of ventriculus.

* All the figures are of adult specimens, and all the sections are drawn from specimens hardened with picro-sulphuric acid or Flemming's fluid, and stained with hæmatoxylin or picro-carmin.

- Fig. 1.—Brain of *Leiostoma palmacinctum* (Oribatidæ), × 240. Sagittal median section, showing the very wide oesophagus passing through the brain and dividing it (in this section) into two halves.
 „ 2.—The same species; sagittal section of brain not median, but taken at the side of the oesophagus, × 240; showing the fusion of the supra-oesophageal and the sub-oesophageal ganglia into one mass.
 „ 3.—Brain of *Cepheus latus* (Oribatidæ), × 175. Sagittal median section.
 „ 4.—Brain of same species, transverse section about the centre of the brain, × 175.
 „ 5.—Brain of *Gamasus terribilis* ♂. Sagittal median section, × 120.
 „ 6.—Brain of *Sejus togatus* (Gamasidæ), × 175. Sagittal median section.
 „ 7.—Brain of *Trombidium* (sp.) probably *holosericeum*, × 175. Sagittal median section.
 „ 8.—Brain of *Trombidium fuliginosum* Herm., seen from above, × 110.
 „ 9.—Brain of *Tetranychus lutearius* (Dufour), × 300. Sagittal median section.
 „ 10.—Brain of *Thyas petrophilus* (Hydrachnidæ), × 120. Sagittal median section.
 „ 11.—Brain of *Cheyletus flabellifer*, × 250. Sagittal median section.
 „ 12.—Brain of *Glyciphagus platygaster* ♀ (Tyroglyphidæ), × 175. Sagittal median section.
 „ 13.—Brain of the same species and sex, × 175. Transverse section about the centre.
 „ 14.—Brain of the same species ♂, × 175. Transverse section about the centre.

* This Journal, 1883, pp. 1–25.

† London (Ray Society), 1884, 1888.

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The Brain in the Acarina

degree of excellence which it has now arrived at ; and these minute Acari, which are possessed of a chitinous exo-skeleton, almost as hard and as brittle as glass (a peculiarity noticed long ago by v. Siebold *), had baffled my attempts to get any sections of them which were at all satisfactory or reliable ; and it is by sections that most can be learned respecting the brain and nerves of such extremely small animals. I allowed the matter to rest, hoping that improvements in apparatus and technique might some day enable me to do what I had not succeeded in doing at that time. The difficulty still exists, the chitin is so hard and brittle that instead of being properly cut, it either takes a notch out of the edge of the razor, or else breaks into numerous pieces at the first touch of the edge, and some of these pieces being carried before the razor, are apt to tear and destroy the soft internal organs which we wish to see ; nor have I found softening agents of any service ; if eau de Labarraque or eau de Javelle be employed I have found that the internal organs are destroyed before the chitin is softened. In spite of these difficulties I have by the skilful assistance of Mr. M. J. Michael of Davos, and with the aid of modern improved microtomes, been able to obtain some sections which at all events show what the brain is really like a great deal better than can be done otherwise ; and as there are not, as far as I know, any existing records on the subject, except the very imperfect information which will be found in my own works above referred to, I think it may be worth while to notice the brain, although I am not able at present to follow it up, as should be done, by a description of the nerves which proceed from it. The reason of this inability is somewhat strange ; it is simply that I have not, as yet, succeeded in seeing these nerves in any way fit for reliable investigation. It is curious, that even the larger nerves, such as those innervating the legs—which are easily seen, and are even conspicuous, in many Acarina far more sluggish than the Oribatidæ, which, although rather slow in their rate of progress, are not really sluggish animals—are difficult, or impossible to see in the Oribatidæ ; even when one does get a good series of sections, or a good dissection, of the brain. Thus, in the crawling Water-Mite *Thyas*, which will be referred to later on, not only are the nerves to the legs large and easily traceable, but I have been able to distinguish and follow the very much smaller nerves to the mandibles, dorso-ventral muscles, and many other quite fine nerves, besides the more substantial ones to the palpi and eyes ; yet *Thyas* is a creature living under stones in the water, or in chinks of the rock, and moving but little, while most of the Oribatidæ are fairly active creatures. The nerves of the latter must be very delicate to escape observation, they ought at all events to be seen where they start from the brain if they were not of extreme tenuity.

* 'The Anatomy of the Invertebrata,' English translation, Boston, 1854, p. 368, note 1.

The so-called brain, or great nervous ganglion, of an Acarus is doubtless derived from a supra-cesophageal ganglion united by broad commissures to a sub-cesophageal ganglion; but, as in many other Arachnida, the fusion of the parts has been so complete, and the commissures have become so broad and short, that the original formation is lost, and the whole appears to be one ganglionic mass, which is penetrated by the cesophagus; still, in the Acarina, the traces of the original distinction between the supra- and sub-cesophageal ganglia are plainly seen in some families, while they are completely lost in others; this produces a considerable variety in the form of the brain, although all are upon the same principle. I propose shortly to refer to these differences in this paper, and also to endeavour to indicate something of the comparative size of the great nervous centre in selected specimens of a few of the great families.

The brain of the Oribatidæ is constructed upon the same principle as the brains of other Acarina which have been described; but the first difference which strikes the observer is the very much greater proportionate size of the opening through which the cesophagus passes as compared with that in the brain of other families; this will be readily seen on comparing fig. 1 of the brain of *Leiosoma palmicinctum* (Oribatidæ) with, for instance, fig. 5, which is that of *Gamasus terribilis* (Gamasidæ). The reason for this is obvious; the Oribatidæ are vegetable feeders and devour a considerable quantity of solid food; the Gamasidæ, and most of the families in which the brain has been described, are predatory creatures, living entirely by sucking the blood of their victims, and never swallow anything except liquid; it is evident therefore that the Oribatidæ would require a much larger cesophageal passage than the Gamasidæ or the Trombididæ. The only other family yet investigated in which the opening in the brain for the passage of the cesophagus is anything approaching the size that we find in the Oribatidæ is that of the Tyroglyphidæ (see fig. 12, *Glyciphagus platygaster*), and these again are vegetable feeders and eat solid food, their food being mostly consumed in a dry state; still, the opening even in the Tyroglyphidæ is not so large as in the Oribatidæ. Of course in this, and all similar remarks in this paper, when I speak of the characters of the brain in a family it must be understood to mean in such species of that family as have hitherto been examined, including those dealt with in this paper.

The next character which will be observed, and it is a very strongly marked feature in the two species which I have good sections of, is that while in most of the known families the greatest measurement of the brain is in an antero-posterior direction (see figs. 5, 6, 7, &c.), in the Oribatidæ this is far the smallest of the three dimensions, while the depth considerably exceeds both the length and the width; this produces a sort of shield-shaped brain on edge in the body. This form does not follow that of the body of the creature; it

is true that *Leiosoma palmarinectum* (figs. 1, 2) is a round-bodied creature, but the form is practically the same in *Cepheus latus* which is not by any means round-bodied. Some of the Hydrachnidæ are very round and short-bodied, much more so than any of the Oribatidæ, and yet the antero-posterior measurement of the brain, although short, is considerably larger in proportion than that of the Oribatidæ. I am not able to give the details of one of these forms of Hydrachnidæ in my table as I do not possess good serial sections of one; but Schaub* in his description of *Hydrodroma dispar* gives the long axis as $\cdot 174$ mm., the width as $\cdot 116$ mm., and the thickness as $\cdot 1$ mm.; his long axis practically corresponds with the depth, and his thickness with the length; he states his whole creature to be about 2 mm. long by about $1\cdot 5$ wide, so that the brain is very small, but Schaub does not give the depth of the whole creature.

A third point to be noticed is that the cortical layer of small, rounded, deeply-staining cells, which usually constitutes the exterior of the brain in Acarina, is thick in the Oribatidæ, whereas in the Hydrachnidæ it is scarcely traceable, and that the fibrous layer exhibits a much more homogeneous and less fibrillar character than in the Hydrachnidæ, Gamasidæ, and many other families; this may probably be correlated with the slighter development of the nerves in the Oribatidæ. Again, it may be noticed that the oesophagus of the Oribatidæ, in its passage through the brain, is not accompanied by tracheæ, as it is in *Trombidium*, &c. This is doubtless due to the small number of the unbranched tracheæ of the former as compared with the abundant supply of fine tracheæ found in the latter.

I will now shortly glance at the relative form and comparative size of the brain in a few of the different families; and the first observation that occurs is that the form of the brain seems to follow the family far more than it follows the shape of the individual species, just as before remarked in the Oribatidæ. Thus the Trombididæ and the Hydrachnidæ are closely allied families, and on reference to figs. 7, 8, 10, it will be seen that the brains are all more or less of an approach to a globular form, notwithstanding that the creatures are very different in shape, *Thyas*, fig. 10, being flattened dorso-ventrally as compared with such a *Trombidium* as *fuliginosum*, fig. 8. *Cheyletus*, fig. 11, is also generally considered to be an allied form, but there are very considerable anatomical differences, and here the brain shows a tendency to lose its sub-globular form and approach a little to that found in *Gamasus*. *Tetranychus*, fig. 9, also is classified as an allied form, but it is a vegetable feeder, and there certainly is an approach to the form of the brain in other vegetable feeders, as will be seen by comparing it with the Tyroglyphidæ (fig. 12), which lead up to the extreme form found in the Oribatidæ.

* "Über die Anatomie von *Hydrodroma* (C. L. Koch), ein Beitrag zur Kenntniss der Hydrachniden," Sitzungsab. d. k. Akad. d. Wiss. Wien, March 1888, Bd. xcvii. Abth. i. pp. 98-151.

The shape of the brain in the Gamasidæ, with its great extension in an antero-posterior direction along the cesophagus, is very characteristic, fig. 5; *Gamasus terribilis* is very like that given by Winkler in his pl. iii. fig. 9, for another species of *Gamasus*, and the extent to which the sub-cesophageal ganglion is developed backward as compared with the supra-cesophageal is a well-marked feature; this is not found in the brain of *Sejus togatus*, but this is a very aberrant species—and the main character of the *Gamasus* brain, viz. its extension along the cesophagus, is well maintained.

Finally, it may be interesting to compare the size of the brain in the different families of Acarina. I have given at the end of this paper a table showing the relative size of the brain to the whole creature in selected species from some of the principal families and sub-families, and I have given in the plate drawings of median sagittal sections of the brain in all these species. I have purposely, in most cases, selected species where the brains have not previously been figured, as adding more to the general stock of information than if I had copied such few figures as exist by other authors. I was of course confined to those species of which I happen to possess good serial sections. The linear measurements have all been carefully made by me from such sections, and may, I think, be relied on as fairly correct. In every instance the measurements of the brain and the whole creature have been made from the same individual.

The calculations of volume can only be considered as approximations. I am indebted for them entirely to the kindness of Mr. E. M. Nelson, who has carefully prepared them from my measurements and drawings; the last three columns of the table are entirely Mr. Nelson's work, not mine. Of course, to obtain absolute correctness as to the volume of such irregularly shaped microscopic bodies as the brains of Acarina, and the Acarina themselves, it would be necessary to follow Mr. E. T. Newton's plan of drawing each one of the series of sections greatly enlarged to scale upon sheets of material of proportionate thickness, and then cutting out the various drawings and joining them so as to obtain a model of substantial size; if this model be made in material heavier than water the model could first be weighed in air and then in distilled water at a known temperature; the difference between the two weights would give the weight of water displaced; from which its bulk could be calculated; or a mould could be prepared from the model and filled with sand, which could be measured. This is the exact method, but it would be immensely laborious where there are a considerable number of figures, such as those included in the table; moreover, although the brain, which is a solid organ, would probably give a correct model by this process, the whole creature undergoes shrinkage and expansion under the action of the reagents necessary to prepare it for section-cutting, and its form gets more or less altered, so that the model of the whole creature would only be an approximation after all, probably not more

exact than what Mr. Nelson has prepared from the measurements and drawings. I think it probable that if an actually correct model of the whole creature, with all its indentations, could be obtained, the brain would bear a slightly larger proportion to the bulk of the animal than that given in the table.

The species selected are not any of them very active. I wished to avoid the difference which might possibly arise from the larger nerve-supply required by a very active creature, and to compare members of the different families as far as possible unaffected by this cause of divergence. Thus, while some Gamasidæ, e. g. *Hæmogamasus hirsutus*, are extremely active, *Gamasus terribilis* is not, although the two species are found together under precisely similar circumstances; and though many Trombidiidæ, e. g. *Erythræus*, and some Hydrachnidæ, are extremely active, yet *Trombidium* and *Thyas* are not; again some Trombidiidæ are very active, but *Glyciophagus platygaster* is not.

It will be seen from the table, which doubtless is a sufficiently close approximation for practical purposes, that the ratio of the brain to the body is lowest in the Tyroglyphidæ, .19 per cent.; this is interesting because they are atracheate creatures, and have always been considered the lowest organisms of any family in the table. On the other hand, the Gamasidæ show far the largest proportion of brain of any of the great families; the ratio of volume of brain to body in *G. terribilis* being 1.61 per cent. Megnin, many years ago, when the size of the brain was quite unknown, asserted that the Gamasidæ were the most highly organised of any of the Acarina; certainly the size of the brain in such a species as *G. terribilis* is very remarkable: it will be seen from the table that the brain is over a fifth of the length, over a fourth of the width, and over a half of the depth of the entire creature; it is however of irregular form, which somewhat diminishes its volume.

The small size of the brain in *Trombidium* and the Hydrachnidæ is not so easily accounted for; here it will be seen it only amounts to about a tenth of the length, a seventh to a fifth of the breadth, and a fifth to a third of the depth, while the volume is not much more than in the Tyroglyphidæ; yet these are rather highly organised creatures, with well-developed eyes, which are absent in the other families quoted. The much larger proportionate size of the brain in *Tetranychus*, which has generally been supposed to be closely allied to the Trombidiidæ, is also difficult to explain. The brain in the Oribatidæ is small when compared with the Gamasidæ, but is considerably larger in proportion than that of the Trombidiidæ and Hydrachnidæ.

It may be worth mentioning the usual ratio of the brain to the body in the human race. In a series of 278 cases weighed by Sims, Glendinning, Tiedemann, and Reid, the maximum weight of the brain in the adult male was 65 oz. and the minimum 34 oz. In

Name of Creature.	Nature of Dimension.	Brain.	Whole Creature.	Proportion of Linear Measurement of Brain to that of Whole Creature.	Approximate Volume		Approximate Proportion of Volume of Brain to that of Whole Creature.
					Of Brain.	Of Whole Creature.	
<i>Cepheus latus</i>	length	·09	1·10	per cent. 8·18	·0008511	·2627	per cent. $\frac{1}{308\cdot6} = \cdot32$
"	breadth	·10	·77	13·00			
"	depth	·21	·55	38·18			
<i>Leiosoma palmarinectum</i> ..	length	·06	·92	6·52	·0005979	·1693	$\frac{1}{283\cdot3} = \cdot35$
"	breadth	·11	·65	16·92			
"	depth	·19	·52	36·65			
<i>Glyciophagus platygaster</i> ♀ ..	length	·12	·75	16·00	·0001772	·9115	$\frac{1}{514\cdot4} = \cdot19$
"	breadth	·09	·65	13·85			
"	depth	·03	·30	10·00			
<i>Gamasus terribilis</i> ♂ ..	length	·35	1·65	21·21	·001	·6175	$\frac{1}{61\cdot75} = 1\cdot61$
"	breadth	·26	1·00	26·00			
"	depth	·31	·57	54·39			
<i>Sejus togatus</i>	length	·16	·90	17·77	·0006184	·065	$\frac{1}{100\cdot25} = 1$
"	breadth	·12	·40	30·00			
"	depth	·09	·22	40·91			
<i>Trombidium</i> sp.?	length	·25	2·40	10·42	·002488	1·2495	$\frac{1}{502\cdot2} = \cdot2$
"	breadth	·15	·82	18·29			
"	depth	·18	·85	21·18			
<i>Thyus petrophilus</i>	length	·11	1·10	10·00	·0004605	·18915	$\frac{1}{410\cdot7} = \cdot24$
"	breadth	·10	·67	14·93			
"	depth	·12	·40	30·00			
<i>Cheyletus flabellifer</i>	length	·07	·52	13·46	·00008776	·01689	$\frac{1}{192\cdot4} = \cdot52$
"	breadth	·07	·28	25·00			
"	depth	·05	·17	29·41			
<i>Tetranychus lintearius</i> ♀ ..	length	·10	·42	23·81	·0001362	·009125	$\frac{1}{67} = 1\cdot5$
"	breadth	·07	·22	31·81			
"	depth	·05	·15	33·33			

All the measurements in this table are in decimals of a millimetre.

a series of 191 cases the maximum weight of the brain in the adult female was 56 oz. and the minimum 31 oz. The mean weight, according to Bischoff, of the adult male brain is 1358 grm. and that of the adult female 1220 grm. In children at birth the average weight according to Boyd is, male 11·65 oz. and female 10 oz., and the proportion of brain to body at birth according to Tiedeman is 1 to 5·85 in the male and 1 to 6·5 in the female; but in the adult the proportion is very much less; in persons dying after prolonged illness probably about 1 to 35; the normal ratio, however, in adult healthy persons is probably about 1 to 45 = 2·22 per cent.

The brain of the Acarina is too small an object to be weighed, but the proportionate weight of the brain to the body would doubtless be larger than the proportionate bulk, because the brain is a solid organ, whereas the body contains large cavities; it would seem therefore that as the human brain averages about 2·22 per cent. of the weight of the body, and the brain of *Gamasus terribilis* measures about 1·61 of the bulk, the brain of that creature, which may be considered a fair specimen of its family, cannot be very far short of the proportion of the human brain.

Note on the Mode of Calculating the Volumes.

By E. M. NELSON, F.R.M.S.

It would seem that the best course to pursue in arriving at the volumes of these irregularly shaped bodies would be to divide them up into more or less regularly shaped portions. Thus, for example, if we take *Cepheus latus* and cut off the rostrum, i.e. the pointed end, we shall have two fairly regular figures to deal with. The volume of the larger portion may be assumed to lie between the volume of an inscribed prolate spheroid and a circumscribed elliptical cylinder. If, therefore, the mean of the volumes of these two figures be taken the result cannot be far from the truth. With regard to the conical end (rostrum), its volume will be larger than a right cone of the same height because of its blunted end, it might therefore be taken as a half instead of as a third of its circumscribing cylinder. Assuming that the length of the conical end is one-sixth that of the whole body, the formula will be as follows:—

Let l be the length, b the breadth, d the depth, and V the volume, then

$$e = \frac{5l}{6}; \quad f = \frac{b+d}{2}; \quad g = b \cdot d \cdot e \cdot \frac{\pi}{4}; \quad h = e \cdot f^2 \cdot \frac{\pi}{6};$$

$$k = \left(\frac{d}{2}\right)^2 \cdot \frac{l}{12} \cdot \frac{\pi}{4}; \quad m = \frac{g+h}{2}; \quad V = k + m.$$

g is the volume of the elliptical cylinder, h that of the prolate spheroid, and k that of the conical end, m being the mean between g and h .

An enlarged model was made of the following dimensions in inches, $l = 2.2$, $b = 1.5$, and $d = 1.1$, this was found to displace 2.02 cub. in. of water. Its volume when computed by the above formula came out as 2.04 cub. in., an agreement sufficiently near for the purposes in question.
