Notes on Parallelism among the Asaphida.*

By PERCY E. RAYMOND, Ph.D.

Presented by LAWRENCE M. LAMBE, F.G.S.
And read May 17, 1911

Isotelus gigas is probably the most common trilobite in the Ordovician rocks of Canada and the United States, and yet it is one of the species of which little is known. It is the custom to group all the smooth asaphids of the Ordovician under this name, but it will probably be found that not more than one half the specimens so labeled belong to this species, and probably one quarter of them belong to other genera than Isotelus. These trilobites are not easily identified, and the attempt to separate the different forms has led the writer to a study of the family. This study has brought together a quantity of data bearing upon the relationships of the various groups.

I am not yet prepared to give a formal definition of the family Asaphidæ, but they may be briefly characterized as opisthoparian trilobites with large head and abdomen shields, prominent eyes, eight segments in the thorax, and always with a median vertical suture in the doublure of the cephalon. The family as thus defined, is less extensive than as defined by Beecher in the American translation of Zittel's Paleontology, and contains 27 genera or subgenera, which are enumerated below.

Ontogeny.

Unfortunately, very little is known of the ontogeny of any member of the Asaphidæ. The nepionic stages of Asaphellus have been described by Matthew, but the series of stages even in this genus is very incomplete. Scattered notes on the ontogeny of Isotelus have been published by Clarke, Walcott, and Raymond and Narraway, while Salter published a few illustrations of immature specimens of Homalopteon and Ogygia corndensis. After a review of what has been published, particularly the work of Matthew on Asaphellus, it seems that the following may be looked upon as primitive characters in this family.—

- 1. Strongly segmented cephalon and pygidium.
- 2. Absence of depressed borders.
- 3. Long glabella.
- 4. Eyes distant from the glabella.
- 5. Facial suture marginal in front of the glabella.
- 6. Pygidium and cephalon short and broad.
- 7. Axial lobe narrow.
- 8. Genal spines present.

^{*}Published by permission of the Director of the Geological Survey.

These primitive characters appear in the genera in various combinations. Ogygiocaris and Ogygopsis have 1, 3, 4, 5, 6, 7, 8; Asaphus and Symphysurus have 2, 3, 5, 6, 7; Ogyginus has 1, 3, 6, 7, 8; Basilicus has 1, 5, 6, 7, 8; Niobe has 1, 3, 5, 6, 7, and so on. On the other hand, certain species of Isotelus lack all these characters, Nileus has only 2, 3, 5; Ptychopyge only 7 and 8; Hemigyraspis has 5, 6, 7, 8; while Asaphellus has only 7 and 8. Judged merely by the above standards, Ogygopsis, Ogygiocaris, Ogyginus, Asaphus, Niobe, Symphysurus, and Basilicus are more primitive than Isotelus, Nileus, Ptychopyge, Hemigyraspis, and Asaphellus.

Hypostoma.

The hypostomas of various species of asaphids have been studied in detail by Brögger, who finds three distinct types. One, typified by Megalaspis and Ogygiocaris, is pointed behind; the second, found in Niobe insignis, is quadrate; and the third, in Asaphus, Isotelus, and other genera, is extended behind into two long, large prongs. The hypostomas of trilobites do not change rapidly, and are therefore important in marking the larger subdivisions in classification. The Asaphidæ can thus be divided into two great groups, according as the posterior margin of the hypostoma is entire or forked. The genera in which the hypostoma is entire are; Ogygopsis, Ogygiocaris, Ogyginus, Asaphelina, Homalopteon, Barrandia, Homoglossa, Ptychocheilus, Niobe (partim), Hemigyraspis, Asaphellus, Megalaspis, Platypeltis, Symphysurus, Illanurus, Nileus, and Voqdesia. In the following the hypostoma is forked; Basilicus, Ogygites, Ptychopyge, Pseudasaphus, Megalaspides, Isoteloides, Isotelus, Asaphus, Brachuaspis, Onchometopus, and Niobe (partim).

It will be noted that in Niobe we have all transitions between the two types. In Niobe insignis the hypostoma is entire, the posterior margin being straight. In Niobe emarginula there is a slight indentation, in N. læviceps it is deeper, and in N. frontalis and in N. explanata the forks are well developed. In geologic position, Niobe insignis is the most ancient and N. frontalis the most recent of these species, and the others appear in the order of the development of the forks of their hypostomas. Brögger has shown this in a table on page 52 of his remarkable paper on the hypostomas of the Scandinavian Asaphidæ.

```
N.\ frontalis. Zone of Megalaspis\ limbata. N.\ explanata. Lower part of same zone. N.\ laviceps. Phyllograptus\ zone. Beekmantown. N.\ emarginula. Ceratopyge\ limestone. N.\ insignis. Ceratopyge\ shale. Top of Cambrian.
```

Within the two great groups indicated by the difference in the form of the hypostoma, the course of development seems to have been from a strongly segmented to a smooth form, and this has given rise to species which are very similar in general aspect, though not closely related. As evidence of this similarity it may be noted that species of Megalaspis, Asaphellus, Onchometopus, and Brachyaspis are commonly referred to Isotelus, and almost any asaphid is referred to Asaphus.

Geologic Range.

The asaphids appear earlier in America, and have a longer range, than in any other country. In the Middle Cambrian at Mount Stephen, Ogygopsis is abundant. At the top of the Upper Cambrian, Illænurus, Symphysurus, Asaphellus, Hemigyraspis, and Megalaspis occur. In the Beekmantown, the asaphids are less varied, as only Isoteloides and Nileus are present. In the Chazy, Isotelus, Isoteloides, Basilicus, Onchometopus, Vogdesia and Nileus occur. In the Lowville and Black River we find Onchometopus, Isotelus, Isoteloides, Basilicus, and Vogdesia. In the Trenton, there are, so far as is now known, only Isotelus and Isoteloides. In the Utica, Isotelus and Ogygites. In the Richmond, Isotelus, Onchometopus, Brachyaspis, and probably Ogygites.

It will be noted that all the Cambrian asaphids belong to genera having entire hypostomas, and that the first genus with a forked hypostoma appears in the Beekmantown. In faunas younger than the Beekmantown, asaphids with entire hypostomas are rare, though they do continue as late as the Black River. Asaphids with forked hypostomas begin to be common in the Chazy, and continue throughout the remainder of the Ordovician.

In the British Isles, the oldest asaphids are found at the top of the Cambrian, (Tremadoc), where Symphysurus, Platypeltis, Ogygiocaris, Asaphellus, Hemigyraspis, and Niobe occur. In the Arenig, Niobe and Barrandia are present. In the Landeilo, Ogygiocaris, Ogyginus, Barrandia, Homalopteon, Basilicus, and Isotelus represent the family. In the Caradoc, Isotelus, Brachyaspis, and Basilicus occur.

In the Christiania District of Norway, Symphysurus, Nileus, Niobe, and Megalaspis occur in 3a, which corresponds to the Tremadoc or the top of the Cambrian. In 3b, (Arenig, Beekmantown), Symphysurus, Megalaspis, Niobe, and Megalaspides are present. In 3c, (Lowville and Black River), the asaphids are Symphysurus, Nileus, Niobe, Megalaspis, Ptychopyge, and Asaphus. In 4, Ogygiocaris occurs.

In Russia, no asaphids are known from deposits older than the Ordovician. In the lower zones, B1 to D3, (Black River group), Megalaspis, Megalaspides, Asaphus, Pseudasaphus, Ptychopyge, Nileus,

Niobe, Onchometopus, Ogygites, Isotelus, and Homoglossa are present. In E, (Lower Trenton), Isotelus occurs. In F1, F2, (Richmond), Brachyaspis is the only genus. The correlations of the strata here given for Russia and Norway are those adopted by Bassler in his recent article on the Russian Bryozoa.

It will be noted that in Europe, as in America, the Asaphidæ with entire hypostomas are most numerous in the Cambrian, but that they range rather higher in Norway and Russia than in America and the British Isles. There are several genera of asaphids which are present in Europe which are unknown or very rare in America. In the Baltic region, Asaphus, Pseudæsaphus, Ptychopyge, Megalæspis, and Niobe are represented by many species, and of these genera only Megalaspis is now known in America, and of that genus only two very rare species have so far been described.

The Genus Asaphus.

Brongniart, the first systematic writer upon trilobites, was the author of the genus Asaphus, which is, therefore one of the first founded of the genera. Although a great variety of species have been referred to Asaphus, Asaphus expansus has remained the central type of the genus, and in Europe various genera and subgenera have been proposed, so that no such heterogeneous assemblage of species has been gathered under the genus as in America.

Asaphus expansus is characterized by its short, broad cephalon and pygidium, from which all depressed borders are absent, by the rather prominent glabella which expands toward the front and reaches the anterior margin, the large prominent eyes, the course of the anterior portions of the facial suture, which meet in a point in front of the eye, and the short pygidium, with narrow well-defined axial lobe and smooth pleural lobes.

Lines of Development from Asaphus.

The genus as exemplified by the type-species is well developed in the Baltic region, and numerous species having the above generic characters have been described, most of them from the Ordovician of the Baltic provinces of Russia. The variation seen among the described species is in the direction of the obliteration of furrows on the surface, that is, a further loss of evidences of original segmentation in cephalon and pygidium. Along with this there is a tendency to widen the axial lobe of the thorax, due, probably, to the greater development of the gnathobases of the coxopodites of the ambulatory appendages in the adaptation

to a crawling mode of life.* This leads to a form to which Schmidt has given the generic name *Onchometopus*.

Onchometopus differs from Asaphus in having the glabella less prominent, the axial lobe of the thorax wider, the thoracic segments flatter, the axial lobe of the pygidium less convex and without rings. The anterior portions of the facial suture are also somewhat closer to the margin. This leads directly to Brachyaspis, Salter, in which all traces of outline of the glabella is lost, the pygidium is evenly convex, with the axial lobe showing but faintly, and with the anterior portions of the facial suture crowded onto the margin. Both these genera show their relationship to Asaphus in the lack of the depressed border on cephalon and pygidium, the short, wide form of these portions of the carapace, and the large prominent eyes.

Leading on another line of development from Asaphus or an Asaphus-like ancestor we have Megalaspides, Brögger, a trilobite very like Asaphus, with narrow axial lobe, expanding glabella, no depressed border on the pygidium, but with a narrow one on the front of the cephalon. One step beyond this is Isoteloides, Raymond, in which both the cephalon and pygidium have depressed borders, the form is more elongate, and the glabella is only faintly outlined. Directly descended from this is Isotelus, Dekay, a genus in which the axial lobe of the thorax is wide, the glabella and the axial lobe of the pygidium so ill defined as to merge into the general surface of the head. Thus, on both these lines, the final result has been a smooth trilobite, and species of Brachyaspis and Onchometopus are so like Isotelus that the three genera can only be separated by careful study with due regard to their lines of development.

This is one of the more striking cases of parallelism, but all these genera are within the group in which the hypostomas are forked. Other examples are between genera much less closely related, as between *Isotelus* and *Asaphellus* and *Hemigyraspis*, or between *Nileus* and *Brachyaspis*.

Basilicus, Salter, is the most primitive genus among those which have the forked hypostoma, and in many ways it parallels Ogygiocaris, Angelin. The pygidium is strongly ribbed, the facial suture is marginal in front, the glabella is strongly outlined and shows glabellar furrows. From Basilicus, Ogygites seems to have developed. Ogygites is the name given by Tromelin and Lebesconte to replace the Ogygia of Brongniart, that name being preoccupied. The type-species, Ogygia guettardi, proves to have a forked hypostoma, and differs from Basilicus principally in having the facial sutures meeting in a point in front of

^{*} See Raymond, Ottawa Naturalist, Vol. XXIV, p. 132, 1910.

the glabella. The three species of Basilicus described by Schmidt from Russia are not the Basilicus of Salter, but belong to this genus Ogygites. In addition to the difference in the course of the suture, the pygidium in this genus is less strongly ribbed. Ogygites is a close parallel to Ogygia corndensis, the two forms being almost exactly alike in general appearance, in the course of the facial suture, the number of ribs, form of glabella, and otherwise, but Ogygia corndensis, to which I have applied the generic name Ogyginus, has an entire hypostoma.

The next step in the development from Basilicus and Ogygites is seen in the genus Pseudasaphus Schmidt, in which the course of the anterior portions of the facial suture is still further within the margin, the glabellar furrows are less prominent, the pygidium shows fewer traces of segmentation, and the doublure of the pygidium becomes very wide. The culmination of this line of development is seen in Ptychopyge, Angelin, where the eyes are very close to the glabella, the facial sutures far within the border, the glabella short and faintly furrowed, the pleural lobes of the pygidium smooth, and the doublure of the pygidium so broad that it underlies all parts of the pygidium except the axial lobe.

Development in the other Group.

The oldest of the Asaphids is *Ogygopsis*, a representative of the group with entire hypostomas. This genus has even more primitive characters than *Basilicus*, for, in addition to the strongly ribbed pygidium, the long glabella, and the marginal facial suture, it has the eyes very distant from the glabella, and retains the eye-lines.

A direct descendant of *Ogygopsis* is *Ogygiocaris*, Angelin, of the Tremadoc and Llandeilo. This name must be applied to those species which are usually looked upon as typical *Ogygias*, namely *Ogygia buchii* and *O. dilatata*, for it seems that the types to which Brongniart originally applied the name have turned out to be trilobites with forked hypostomas, and the *Ogygias* of England and Scandinavia can not be placed in the same genus with them.

The development in the line from *Ogygopsis* is parallel to that seen in the species with the forked hypostomas, the result being the elimination of furrows from the dorsal surface of the crust. Unfortunately, however, there seem to be many gaps in the line of development, and we have mostly the terminal and widely separated results of the process, with few of the connecting links.

There seem to be three lines diverging from the *Ogygopsis* stock; one in which the glabella remains long and the head short and wide, leading to *Nileus*. In a second, the cephalon becomes elongate, the

glabella short, and the suture intra-marginal, thus producing *Megalaspis* and *Asaphellus*. In the third line the suture remains marginal, but the dorsal furrows become obsolete, and the result is *Hemigyraspis*, a close parallel in its smoothness to *Isotelus* and *Asaphellus*.

Thus we have six genera of smooth trilobites, all belonging to the Asaphidæ, all similar in general appearance, but developed along separate lines and not closely related. These genera are Nileus, Hemigyraspis, Megalaspis, Asaphellus, Brachyaspis, and Isotelus.

Following out the development of the first group, we find no connecting link between Ogygopsis and Platypeltis, Callaway, unless it be the species described by Schmidt as Ogygia dilatata panderi, a form which is, unfortunately, known from only one imperfect specimen. It is evidently not an *Ogygiocaris*, and has a long glabella with glabellar furrows at the sides, a distinct but smooth axial lobe on the pygidium. and smooth pleural lobes. I have called this *Homoglossa*. It appears to be near *Platypeltis*, Callaway, which has the glabella extending to the front, no marginal depression along the borders, and a smooth pygidium, on which, however, the axial lobe is fairly prominent. The axial lobe of the thorax is narrow. From this it is only one step to Symphysurus, Goldfuss, this genus differing from the preceding principally in lacking the genal spines. Through the broadening of the axial lobe and the flattening of the glabella and the axial lobe of the pygidium. Nileus, Dalman, was developed from Symphysurus, and we have a line parallel to that proceeding from Asaphus to Brachyaspis, the two groups being similar in their short, wide cephalons, incurved profile, and long glabellas, but radically different in their hypostomas.

In the second line, Ogygia corndensis, which I have called Ogyginus, forms a link between the Ogygopsis-Ogygiocaris line, and Megalaspis, Angelin. Ogygia corndensis has an intra-marginal facial suture, a glabella flatter and shorter than in Ogygiocaris or Ogygopsis, and fewer segments showing in the pygidium. Ptychocheilus, Novak, if correctly described, is intermediate between Ogygia corndensis and Asaphellus, Callaway. Ptychocheilus, as described by Novak and by Brögger, has an intra-marginal facial suture, a distinct glabella and axial lobe on pygidium, and ribs on the pleural lobes of the pygidium. Asaphellus has the intra-marginal suture, a glabella so faint as to merge into the general surface of the cranidium, and a smooth pygidium, but retains the primitive narrow axial lobe and genal spines. It is, nevertheless, a close parallel to Isotelus, and is not always readily distinguished from that genus, especially as the more primitive and phylogerontic species of Isotelus have a rather narrow axial lobe.

Megalaspis could hardly have developed from either Asaphellus or Ptychocheilus, but its close relation to Ogygiocaris is shown in the fur-

rowed ribs which are faintly visible on the pleural lobes of the pygidium. This genus is extremely variable, the cephalon and pygidium varying. from almost semi-circular to distinctly triangular. The glabella is short, the suture intra-marginal, and the hypostoma pointed behind. Many of the species are very smooth and very similar in appearance to *Isotelus*.

In the third line, with the facial sutures marginal, Homalopteon, Salter, is intermediate in the matter of segmentation between Ogygopsis and Barrandia, Salter, and Barrandia in turn is less smooth than Hemigyraspis, Raymond, but this can hardly be a correct line of descent, as Hemigyraspis occurs in strata much older than those in which the other two genera are found. Niobe, Angelin, probably descended from the same stem as Hemigyraspis, but is much more primitive in its long and distinct glabella, and the possession of ribs on the pleural lobes.

Niobe is an especially interesting genus, as it seems to represent a form which stands near the stem from which all the Asaphidæ with forked hypostomas sprang. By supposing two lines of development to have proceeded from Niobe, one in which the primitive characters of short head and long glabella are accentuated, and the other in which the opposite is developed, we may get all the forms seen in this group.

Explanation of Plates.

Plate 1.

- 1. Brachyaspis notans, (Billings). A photograph of the type, showing the absence of depressed borders, the short and wide cephalon and pygidium, and the forward-expanding glabella of an Asaphus. The facial suture is, however, marginal in front, and the axial lobe is wider than in Asaphus. A phylogerontic feature shown in this species is the presence of genal spines. The specimen is from the Richmond formation at English Head, Anticosti, and is number 2180 in the Museum of the Geological Survey.
- 2. Ogygites canadensis, (Chapman). A specimen from the Utica at Collingwood, Ontario, to show the strongly ribbed pygidium, the narrow axial lobe, and the genal spines. The specimen is exfoliated in front, so that the course of the facial suture is not shown. C. G. S. Mus. No. 1934.

Plate 2.

1. Onchometopus susæ, (Whitfield). Profile view of a specimen to show absence of depressed border. This figure also shows the course

of the facial suture, which is just within the margin in front of the glabella. The specimen is from the Richmond at East Selkirk, Manitoba. G. C. S. Mus. No. 7170.

- 2. The same specimen. Another view to show the short, wide cephalon, the wide axial lobe, and the large eyes.
- 3. Brachyaspis alacer, (Billings). Photograph of the type, to show the marginal facial suture, the obsolete glabella, and the depressed eyes. The specimen is from the Richmond at Charleton Point, Anticosti. C. G. S. Mus. No. 2179.
- 4, 5. Brachyaspis altilis, Raymond. (Nomen nov.) Anterior and dorsal views of the type to show the marginal facial suture, obsolete glabella, and wide axial lobe. This is the specimen figured by Billings in the "Catalogue of the Silurian Fossils of Anticosti," p. 26, fig. 9b, as Asaphus platycephalus. From the Richmond at English Head, Anticosti. C. G. S. Mus. No. 2181.
- 6. Megalaspis goniurus, (Billings). A photograph of one of the types. The specimen is from the conglomerates at Point Levis, and the Museum number is 830.
- 7. Isotelus gigas, Dekay. Profile view of an enrolled specimen for comparison with Fig. 1. The depressed border is present. This specimen is from the Trenton at Hull, Quebec, and is in the Museum of the Geological Survey. (Stewart collection).
- 8. Nileus perkinsi, Raymond. Photograph of a cephalon for comparison with *Brachyaspis* and *Onchometopus*. Note absence of depressed border, obsolete glabella, and marginal facial suture. This specimen is from the Chazy at Isle La Motte, Vermont, and is in the U. S. National Museum.
- 9. Isotelus gigas, Dekay. This figure is introduced to show the long, sub-triangular outline of the cephalon, even in a flattened specimen. Note the very wide axial lobe. This specimen is from the Trenton at Lake Winnipeg, Manitoba, C. G. S. Mus. No. 1798.

Plate 3.

1. Nileus perkinsi, Raymond. Photograph of the underside of the doublure of the cephalon, to show the vertical suture. It has been repeatedly stated that this suture is not present in Nileus and Symphysurus, but it is present in Nileus perkinsi and Symphysurus illænoides. In other respects the genera mentioned are close parallels of Bumastus and Illænus. The specimen here figured is the same one shown in figure 8 of the preceding plate.

- 2. Onchometopus obtusus, (Hall). A specimen from the Chazy at Isle La Motte, Vermont. In the collection at the University of Vermont.
- 3. Bumastus globosus, (Billings). A photograph by Professor George H. Hudson of a specimen in his collection from the Chazy at Valcour Island, New York. Introduced for comparison with Nileus and Brachyaspis.
- 4. Nileus affinis, (Billings). An enrolled specimen from the conglomerates at Point Levis, Quebec. The type of the species. C. G. S. Mus. No. 889.
- 5. Symphysurus illænoides, (Billings). A photograph of the type, for comparison with Nileus. C. G. S. Mus. No. 832.
- 6. Isotelus gigas, Dekay. A specimen from the Trenton at Cobourg, Ontario. Notice the long triangular cephalon of this species, and the depressed border. C. G. S. Mus. No. 1786.
- 7. Hemigyraspis sp. A form very similar to H. planus, (Matthew). The cephalon and pygidium are short and wide, the facial suture is marginal in front, and the axial lobe is rather narrow. The specimen might easily be taken for an Isotelus. It is from a locality three miles east of Golden, in the Kicking Horse Pass, B.C., and was collected by Mr. R. G. McConnell.



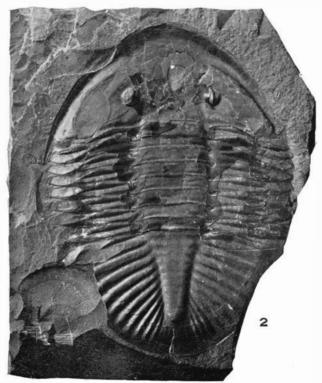


PLATE I.

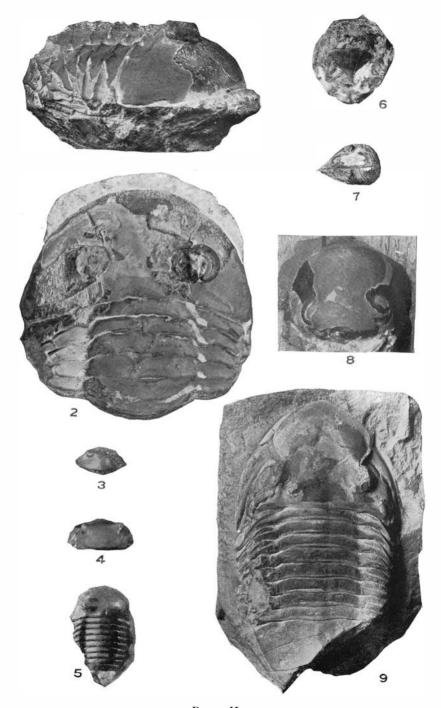


PLATE II.

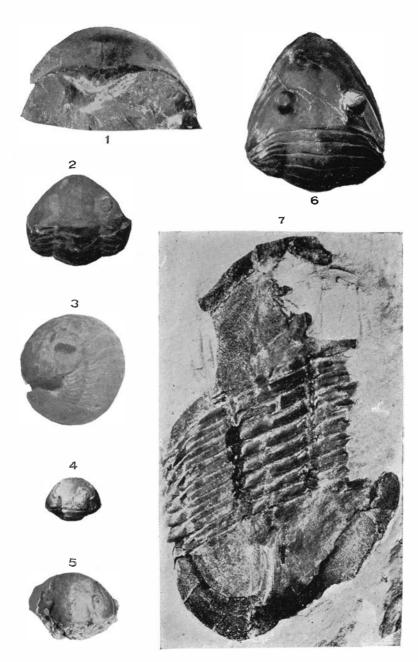


PLATE III.