Proceedings of the Iowa Academy of Science

Volume 57 | Annual Issue Article 33

1950

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The earliest fossil fragments which have been positively identified as vertebrate come from the Upper Ordovician. They are fragments, the best known of which come from the Harding sandstone near Canon City, Colorado. Though fragmentary, study of the histological structure of the plates indicates that they were bony, therefore vertebrate, and that the bone structure agrees with that in the shields of the Heterostraci, one of the orders of Ostracoderms. (1) These are intriguing fragments, hints of the presence of vertebrates but inadequate to give us any idea of the body form or of any details of structure.

Following this early occurrence the fossil record is a blank through-out the long period between this and Upper Silurian. When the next record available thus far is examined it is found to contain a wealth of Ostracoderm forms. It is this next occurrence which I wish to discuss. I could only wish that I might be able to sketch the history of the group between Upper Ordovician and Upper Silurian, for somewhere in the rocks of that interval must lie the records of a very important chapter in vertebrate evolution.

The stratigraphic data on the Silurian horizons from which Ostracoderms have been recovered has been summarized by Heintz (2) and by Westoll (3). They agree in the order of occurrence, although differing slightly in some details. That order is as follows:

Trematapis beds, Oesel, Estonia: Lower to Middle Ludlow;
Skane, Sweden: Probably Middle to Upper Ludlow;
Lesmahagow, Scotland: Middle to Upper Ludlow;
Rudstangen, Norway: Upper Ludlow;
Cowie Harbor, Scotland: Basal Downtonian;
Welsh Border: Lower Downtonian.

The Silurian occurrences appear all thus far in northwestern Europe and the British Isles. Devonian occurrences are widely scattered, in areas from Germany, Poland, Russia, Spitsbergen, East Greenland, Quebec, Pennsylvania, Colorado, and Wyoming, to mention some of them. Thus far the group is unknown after Upper Devonian.

The Oesel deposits have been known for at least a century. Pander (4) in 1856 published a paper in which he described and named 28 genera and 42 species, mostly based on minute fragments of bony plates and on isolated Coelolepid scales. Many of his genera and species cannot be adequately identified and have

been discarded. Since that time quite a few workers have collected from and described the Oesel quarries. Among those whose explorations have been most successful was Dr. Wm. Patten, of Dartmouth College. Dr. Patten made four trips to Oesel, the last two of which were by far the most fruitful. He returned from the last trip in September 1932 and died a month later, leaving his extensive Ostracoderm collection almost unanalyzed taxonomically. That task I took over after his death. It has proved a fascinating research field and has resulted in demonstration of an extensive radiation of the Ostracoderms by Upper Silurian times.

The Ostracoderms, the oldest known vertebrate group, are armored creatures, the armor being made of bone, either as a series of scales or of plates or as a solid encasement of the anterior part of the body. While taxonomic procedures vary somewhat, it is a fairly accepted practice among students of this group to place them, together with the modern Cyclostomes, in a special group, the Agnatha, sometimes ranked as a Super-class, the remainder of the vertebrates being placed in the Gnathostomata. The position of the Cyclostomes in the classification varies. The fossil forms, in any case, are placed in the class Ostracodermi, usually including the modern forms, and this class is divided into two sub-classes, the Pteraspidomorphi and the Cephalaspidomorphi, each of which is further split into orders, Heterostraci and Coelolepidae in the Pteraspidomorphi, Osteostraci and Anaspida in the Cephalaspidomorphi.

The paleontological interest in the group is that as the earliest known vertebrates they should be of help in the problem of vertebrate origin and also in the problem of the stem form or forms from which have arisen the Gnathostomes which have radiated out into the varied vertebrate assemblage revealed by the records in rocks of Devonian to recent times as well as those of today.

The Oesel deposits contain representatives of both sub-classes of Ostracoderms. Many of Pander's genera and species were founded on isolated scales of Coelolepids. There is some variation in the scales of individual animals, and it is probable that Pander erected two or more species in scales which really belong to different regions of the body of the same species. However, discounting many such species, we at least know that Coelolepids occur in the deposits (5) (Heintz-Kiaer 1932). A representative of the other order of Pteraspidomorphi, Tolypaspis, has also been reported (2).

The Cephalaspidomorphi of Oesel have been more extensively dealt with. In this group also both orders are represented. The

Anaspida have been rather fragmentary but appear to belong to a different genus from the Norwegian forms described by Kiaer (6) and have been given the generic name Saarolepis (7, 8). In the Anaspida the body and head are both encased in scales, and it is thus rare to find more than scattered fragments.

It is the shield-bearing Osteostraci which are best represented in the collections. In these either the major part of the head or parts of both head and trunk are encased in a bony shield. Taxonomic distinctions are based on shield characters. Five families of this order have been recognized (9). Four of the five occur in the Oesel deposits. Three of them, Trematapidae, Dartmuthiidae, and Oeselaspidae were described from Oesel and, except for the possibility that some fragments described from Skane, Sweden by Lehman (10) may be Trematapids, are not known from other localities.

The taxonomic list which follows includes only those species which appear at present to be valid:

Subclass Pteraspidomorphi
- Order Thelodonti
  - Family Coelolepidae
    - Coelolepis luhai Kiaer-Heintz
- Order Heterostraci
  - Family Cyathaspidae
    - Tolypaspis

Subclass Cephalaspidomorphi
- Order Anaspida
  - Saarolepis oeselensis Robertson
- Order Osteostraci
  - Family Cephalaspidae
    - Cephalaspis oeselensis Robertson
    - Thyestes verrucosus Eichwald
    - Saaremaaspis mickwitzi (Rohon)
    - Witaaspis schrenckii (Pander)
    - Witaaspis patteni Robertson
  - Family Dartmuthiidae
    - Dartmuthia gemmifera Patten
    - Rotsikullaspis obrutchevi Robertson
  - Family Oeselaspidae
    - Oeselaspis pustulata (Patten)
  - Family Tematapidae
    - Trematapis schmidti Rohon
    - Trematapis milleri Patten
    - Trematapis mammillata Patten
    - Trematapis rohoni Robertson
    - Trematapis patteni Robertson
    - Trematapis panderi Robertson
    - Trematapis scalaris Robertson

Two subclasses, four orders, seven families, twelve genera, and eighteen species, to count only those which can be definitely identified, is a remarkable record for this early horizon. This rich assemblage from a few small quarries in a limited area is only a sample of what undoubtedly was a much more extensive deployment of this vertebrate group, and an almost certain indication that we can expect to find a considerable variety of Ostracoderms in still earlier rocks.

This group, moreover, shows variety of form, probably indicative of varied habitat and habit. Most of them were probably bottom-dwellers, for the body is dorso-ventrally flattened. Some others, such as the Anaspids, were more fusiform, probably more active swimmers.

Aside from their significance in these respects, the Oesel fossils have been of importance due to the excellent preservation, which has made it possible to investigate anatomical details such as the form of the brain case in at least one form, Trematapsis, including in this case some features of the nerve and blood vessel channels. Some portions of nerve and blood vessel channels can be traced on others. The lines of the sensory canal or lateral line system have been well preserved in several of the genera. These and impressions of the gill pouches have enabled us to verify still more closely the similarity between these Ostracoderms and the modern Cyclostomes.

I would like to stress again, as I did in a paper before the Academy last year (11), the importance of a thorough exploration of Upper Ordovician and Silurian sediments for traces of this group. Fragments which can not be identified as belonging definitely to any of the invertebrate groups, unusual forms of "Conodonts," etc. may give us some clues. If there is adequate material to enable one to grind some sections it should be possible to determine histologically whether the material is Ostracoderm.

I do not believe we should assume, in examining these sediments, that only those of fresh water origin might hold Ostracoderm remains, for it is still a moot question whether vertebrates as a group arose in fresh or marine waters.

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