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An early Ordovician vertebrate

HETEROSTRACAN fishes are the oldest known fossil vertebrates, and well preserved examples are frequently found in rocks of late Silurian and Devonian age, but in older rocks their remains are fragmentary and rare. Their oldest occurrence yet described is in the Harding Sandstone, Colorado (middle Ordovician[1,2]), where two genera occur; one of these has subsequently been recognised in marine limestones of similar age from Ontario, Canada[3].

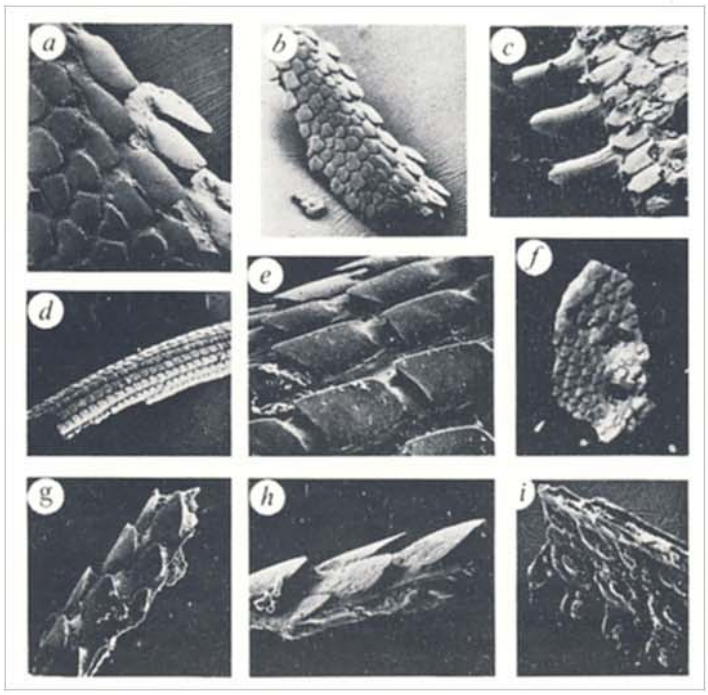

Fig. 1 Fragments of *Anatolepis heintzi* (*a–f*, *i*) and *Anatolepis* sp. (*g* and *h*) from the early Ordovician Valhallfonna Formation, northern Spitsbergen. *f* Was taken with a light microscope, the others with a scanning electron microscope. *a* and *b*, Holotype, PMO NF 3263/1 (×54 and ×18, respectively), showing typical scale types with smooth external surfaces; *c*, PMO NF 3263/2, part of spine-like fragment (×36), with transformed scales at edge; *d* and *e*, PMO NF 3263/3, elongate, U-shaped fragment with rhombohedral external scales (×18), and detail (×180); *f*, fragment with obliquely orientated, circular perforations, PMO NF 3263/4 (×18); *g* and *h*, PMO NF 3263/5, fragment of second species of *Anatolepis* with grooved scales; *g*, from above (×30); *h*, lateral view (×94.5); *i*, inner surface of a fragment, PMO NF 3263/6 (×54), showing low tubercles perforated at tip, and trilaminate structure at broken edge.

During the search for phosphatic microfossils from the early Ordovician Valhallfonna Formation, northern Ny Friesland, Spitsbergen[11], we recovered numerous small fossils which are identified as fragments of the earliest heterostracan, indicating that the earliest vertebrate occurrence predates that of the Harding Sandstone by about 20 Myr.

Whereas deposits containing later heterostracans were laid down in freshwater or brackish conditions[4], the earliest sediments are regarded as fully marine, indicating that the vertebrates had their origin in the same medium as other major metazoan groups[5,6]. The only recorded occurrence of vertebrate remains supposedly pre-Middle Ordovician are some small thelodont denticles—termed *Palaeodus* and *Archaeodus*—from the early Ordovician of the Russian platform[7]. These specimens are lost, and doubt has been cast on their authenticity (ref. 3 and S. Turner, personal communication). The Middle Cambrian problematicum *Eoichthys* Bryant[8,9] is regarded as unlikely to be vertebrate; indeed it was later[10] not considered as such by its original author.

The present finds were part of residues obtained by dissolving limestones in acetic acid, which otherwise include conodonts, chitinozoa[12], trilobites, brachiopods and radiolaria[13]. The associated fauna indicates a shallow shelf, fully marine environment, with a well oxygenated, soft, muddy sea floor, populated by a variety of benthic trilobites[14]. Vertebrate remains have been recovered from two horizons: 90–100 m from the base of the Olenidsletta Member and

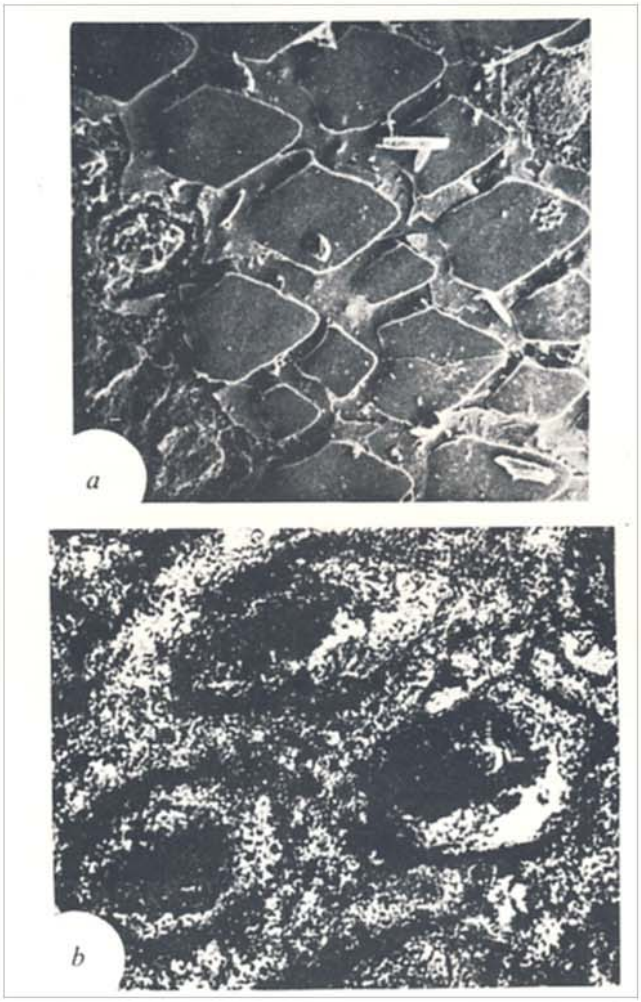

Fig. 2 *Anatolepis heintzi a*, PMO NF 3263/7 (×300). Scanning electron microscope photograph of part of fragment showing circular structures beneath each scale; *b*, PMO NF 3264 (×1,600), light microscope picture of similar fragment to *a*, photographed with transmitted light to show circular aspidin structures in middle of scales (NF 15, Fig. 10).

30–50 m from the base of the Profilbekken Member. The former occurrence is with graptolites indicating an Arenig (early Ordovician zone of *Didymograptus hirundo*) age, the latter slightly younger, possibly earliest Llanvirn.

The specimens range in length from 1 to 2 mm, and one or more edges are invariably frayed, suggesting that the fragments are parts of larger plates. Analysis by X-ray diffraction shows that fragments are composed of apatite but the possibility of the hydroxyl (OH) radical being present (in small amounts) cannot be eliminated. The outer surfaces of the plates are covered with minute, smooth, elliptical to rhomboidal scales 25–150 μm long; the larger scales are concentrated at the edges of the fragments, where they are frequently more or less imbricated. Plates are frequently 'doubled over' at the edges with larger scales (Fig. 1*a* and *b*), such fragments possibly being from the

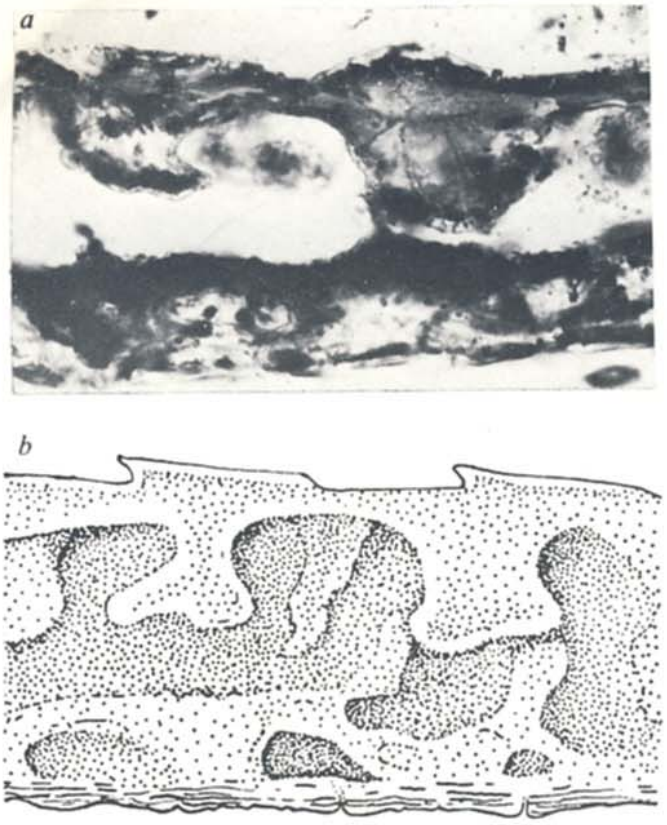

Fig. 3 *Anatolepis heintzi*. *a*, Photograph of thin section of PMO NF 3262 (×750), showing external scales, basal lamellar layer, intermediate cavernous aspidin layer. *b*, Generalised reconstruction of *Anatolepis* bone (×750).

perimeter of the animal (and if this is so, indicating a dorsoventrally flattened overall shape). The inner surface of the plates carry tubercles of two sizes; the larger of these are perforated at their tips, these perforations presumably being the sites of dermal nerves or blood vessels (Fig. 1*i*).

Apart from flat or slightly curved fragments or 'edge' pieces, there are two particularly interesting fragments which, being covered with similar scales, are referable to the same animal. One is a spine (Fig. 1*c*) in which some of the scales are extended to form blades. The other fragment (Fig. 1*f*) includes small, circular openings, each equipped with a small lip externally and doubtless representing original openings in the exoskeleton. Since several groups of early agnathans had separate gill openings it is tempting to assume that these perforations represent the openings into the gill pouches, but they may also be pores into the lateral line system.

The plates are remarkably thin (70–100 μm) and delicate, and this explains why larger fragments have not been recovered. In section the structure of the plates is similar to that described for other heterostracans[15,16], with a basal lamellar layer, an outer, probably dentinous, layer carrying the rhomboidal scales, the two separated by a spongy 'aspidin' layer (Fig. 1*j*, Figs 2 and 3): the latter easily tears during sectioning. Both *Astraspis* and *Eriptychius* from the Harding Sandstone are much more robust and have completely different external tubercles—the latter variously lobate, frequently with broad, subparallel raised ridges, the former with hemispherical, radially grooved tubercles. External tubercles of both these genera have more than twice the average diameter of those of the new material from Spitsbergen. Because of these differences we propose a new name for the species described here—*Anatolepis heintzi* gen. et sp. nov. The type species is named after the late Professor Anatol Heintz, who contributed much to the study of early fishes. A distinctive second species, with minutely grooved external scales (Fig. 1*g* and *h*), has been recovered (one specimen only) from the lower horizon.

More material, preferably still *in situ* on the bedding surfaces, is needed before an attempt at a reconstruction of the whole animal can be made. The fragments alone are of interest because they prove that heterostracans were already present in the earliest part of the Ordovician (500 Myr ago) and show that they were then certainly Marine. They also indicate that the thicker armour of the middle Ordovician forms is likely to have been secondary[17]. Material at hand shows no evidence of cyclomorial growth[18] or fusion of smaller tesserae[19], and it is possible that skeletisation occurred all at once in *Anatolepis* rather than by fusion of individual tubercles. If such fusion occurred it may have been in an ancestor of Tremadocian or Upper Cambrian age. Our discovery may stimulate examination of acid residues of pre-Ordovician age for the remains of still earlier vertebrates.

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