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THELODUS MACINTOSHI STETSON 1928, THE LARGEST KNOWN THELODONT (AGNATHA: THELODONTI)

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ABSTRACT. Material attributed to the thelodont *Thelodus macintoshi* Stetson, from the Silurian of New Brunswick, Canada, is shown to be heterogeneous. It comprises not only the type thelodont, *T. parvidens* Agassiz 1839, but also a species of *Loganella* similar to *L. ludlowiensis* or *L. martinsoni* (Gross 1967) and an acanthodian resembling *Gomphonchus*. Scales of *T. bicostatus* Hoppe and *T. trilobatus* Hoppe are found in association with those of *T. parvidens* for the first time. Measurements of Stetson's type material confirm that *T. parvidens* is the largest known thelodont, with a total length of about one meter. The vertebrate fauna including these thelodonts could be as old as late Llandovery (within the Long Reach Formation) or as young as early Pridoli (in the Jones Creek Formation). The New Brunswick thelodonts are similar in preservation to those from the Lower Silurian fish beds of Scotland, but their phylogenetic affinities are closer to those from the Silurian of England and the Baltic region.

INTRODUCTION

In 1928 Harold Stetson described articulated thelodont material, preserved in calcareous concretions, from a site in the Silurian rocks near Nerepis, Kings Co., New Brunswick, eastern Canada. This was the first definite thelodont material found in North America. The site, at Cunningham's Brook (Cunningham's Creek on the map of MacKenzie 1964), has also yielded the heterostracan *Cyathaspis acadica* (Matthew), (see Denison 1964), spines of an acanthodian related to *Climatius* (Denison 1956, p. 385), and a possible anaspid,

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Ctenopleuron nerepisense Matthew 1907, which remains indeterminate (e.g., Woodward 1920). Associated invertebrates include ceratiocarids, conodonts and a xiphosuran (Denison 1956; Blicek 1982).

MATERIALS AND METHODS

The nodules containing this thelodont material were collected from siltstones by Stetson and W. E. Schevill of the Museum of Comparative Zoology during a Harvard expedition in 1927, following up the lead of William MacIntosh of the Natural History Society of New Brunswick. The type material is housed at the Museum of Comparative Zoology, Harvard University.

Subsequently, during the 1950s and 1960s, Robert Denison (then of the Field Museum of Natural History, Chicago) collected more material from two separate horizons. Denison referred all the thelodonts he collected to *Thelodus macintoshi* Stetson. In 1956 he stated that the specimens came from the Long Reach Formation, following the lead of Matthew (1888) who stated that the fish beds were in the Mascarene Group, Division 2 which was subsequently called the Long Reach Formation (e.g., MacKenzie 1951). In 1964 Denison corrected his statement by referring the *Cyathaspis acadica* material to the Jones Creek Formation, on the basis of MacKenzie's 1951 field appraisal. This interpretation was followed by Blicek (1982).

Evidence, however, from the 1964 maps of the region by MacKenzie suggests that all the fish beds are within the older Long Reach Formation. The position of the two formations has been confused because in the 1950s, and on the 1964 Saint John and Hampstead maps, MacKenzie placed the Jones Creek Formation *below* the Long Reach Formation. In fact, the reverse order is the case (Berry and Boucot 1970; McCutcheon 1981). One recent source places the fish beds definitely within the Long Reach Formation (Smith 1966). In the notes of the 1964 Hampstead map there is even a reference to a new locality in the Long Reach Formation for "a primitive fish" in a brook, northeast of Armstrong Corner. This specimen was not identified and I have no further information about it. It may be that the cyathaspids did not come from the same horizon as the thelodonts and other elements of the fauna.

In the early 1970s, Denison sent me, on request, a sample of loose scales from one of the nodules from the New Brunswick site. I

attempted to make thin sections, but the histological structure of the scales was disrupted by post-mortem algal or fungal attack, or recrystallization (see Pl. 1). In general shape, however, the scales seemed identical to those of *T. parvidens*. I also examined a specimen of *T. macintoshi* in the British Museum (Natural History), collected from New Brunswick by W. Graham-Smith in 1937. On the basis of these investigations, I suggested that *T. macintoshi* was virtually identical to *T. parvidens*, at least in its scale morphology (Turner 1973, 1976). [I also stated that the Long Reach Formation was the stratotype, following Denison 1956; see also Blicek 1982]. From a perusal of Stetson's figures in 1968 I decided to write a paper on the closure of Iapetus, the early Palaeozoic ocean (Turner 1970). For if *T. parvidens* and *T. macintoshi* were the same species, then New Brunswick and the Anglo-Welsh region must have been closely aligned in the late Silurian.

In his original work Stetson (1928, Figs. 1-3) described and figured scales he thought looked like typical *T. parvidens* scales but which bore long thin extensions on the posterolateral rims of the crowns (Figs. 2, 3). This character prompted him to distinguish *T. macintoshi* as a separate species. In spring 1983 I examined both Stetson's and Denison's collections. Specimens PF are housed at the Field Museum of Natural History, Chicago (FMNH), MCZ at the Museum of Comparative Zoology, and BMNH at the British Museum of Natural History.

MATERIALS EXAMINED

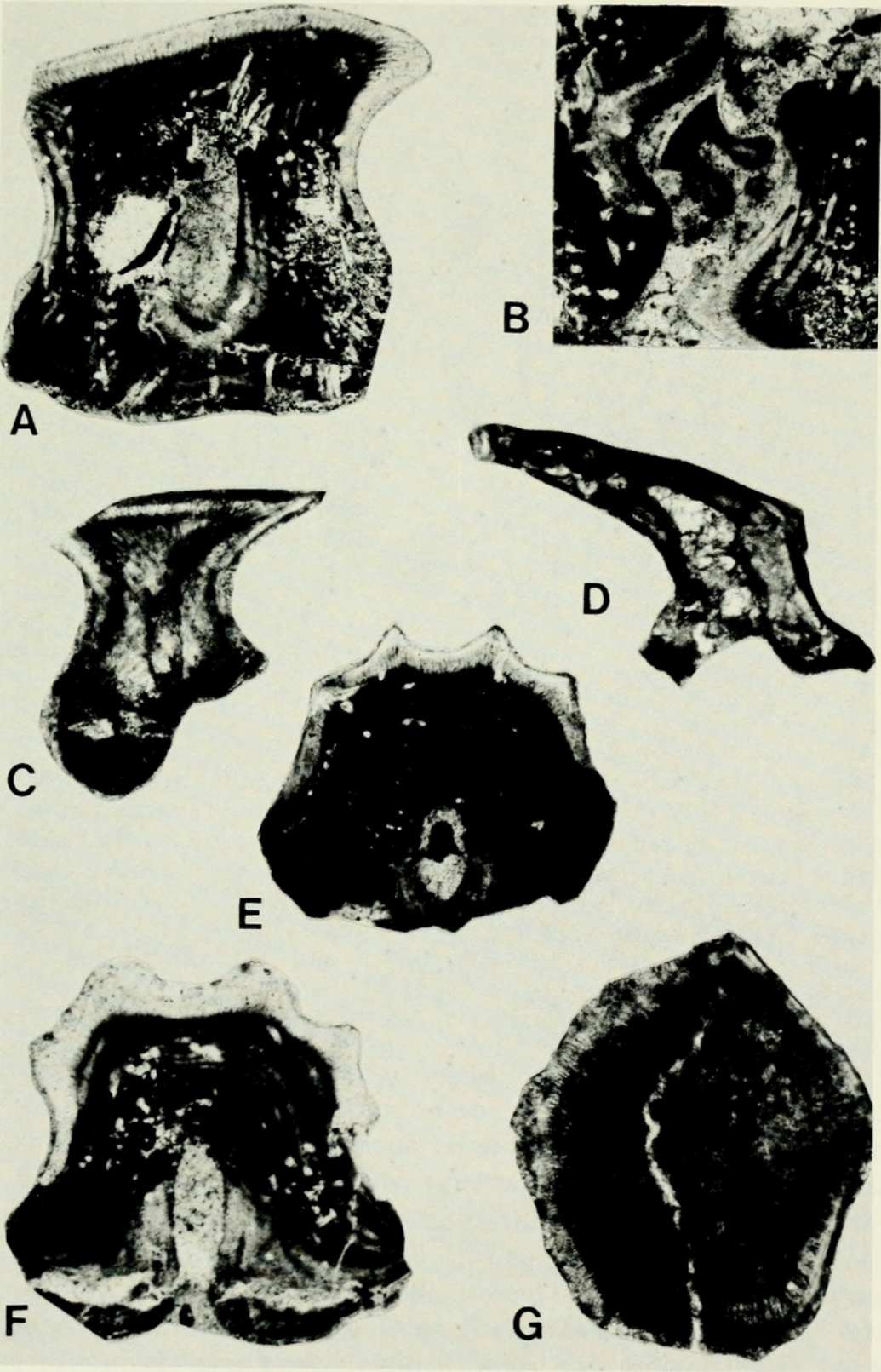
- MCZ 2035 HOLOTYPE *Thelodus macintoshi* Stetson 1928 is *T. parvidens* Agassiz with *T. trilobatus* scale. Area at least 30 + × 250 mm. Holotype includes thin sections.
- MCZ 2037 Paratype *T. macintoshi* is *T. parvidens*.
- MCZ 2036 Paratype *T. macintoshi* is *Loganella* cf. *L. ludlowiensis* (Gross 1967).
- MCZ 13007 in part to 13015, includes the specimens from which some thin sections were cut, are referred to *T. parvidens* Agassiz.
- MCZ 13007 in part; one nodule has *Gomphonchus* type scales.
- MCZ 13014 includes *T. bicostatus* (Hoppe 1931) scales.
- MCZ 13012 is at least 240 mm long.

- PF 1805 *T. macintoshi* is *T. parvidens*, area 300×170 mm (Denison coll.).
- PF 1809 *T. macintoshi* is *T. parvidens* horizon A, area at least 300×170 mm (Denison coll.).
- PF 1804 *T. macintoshi* is *T. parvidens*, horizon B (Denison coll.).
- PF 1808 loose thelodont scales in coprolite includes *T. parvidens*, *T. bicostatus* and *T. trilobatus*, horizon B.
- PF 1803 is a coprolite containing *Gomphonchus* type scales.
- PF 1802 is a coprolite with thelodont scales, *T. parvidens*, horizon B.
- PF 3475 jumbled *T. parvidens* scales in coprolite, (Denison coll. 1961).
- PF 3476 *T. macintoshi* - a good articulated *T. parvidens*, incomplete 150×90 mm in area (Denison coll. 1961).

PF 3477 and PF 1801 are acanthodians and PF 1698 is an acanthodian ?spine. At least three uncatalogued specimens, including 126-52 and 1969 Denison coll. FMNH, are coprolites from horizon B containing well-preserved *T. parvidens* scales.

BMNH P.52444. *T. macintoshi* (Graham-Smith coll.) is *T. parvidens* with *T. trilobatus*? scales.

Plate 1. Histology of thelodont scales from coprolitic nodules from Cunningham's Brook, Nerepis, New Brunswick (slides prepared at Field Museum, Chicago). A) Vertical section through large scales of *T. parvidens* showing growth lines in orthodentine and invading hyphae, or boring algae; anterior to left, slide 4187; B) Small scale of *T. parvidens* in sagittal section interposed between two larger scales of *T. parvidens*, slide 4187; C) Sagittal section through a scale of *T. parvidens* with a much enlarged anterior base (in the manner of *T. laevis* Pander (see Gross 1967; Karatajute-Talimaa 1978), and the pulp canal; anterior to left, slide 4192; D) Young scale of *Thelodus trilobatus* with large open pulp cavity, in sagittal section; anterior to right, slide 4192; E) Scale of *Thelodus bicostatus* in transverse vertical section showing growth lines, slide 4187. F) Scale of *T. bicostatus* or *T. trilobatus* showing growth lines and invading hyphae or algae, slide 4187; G) Horizontal section through crown of *T. parvidens* scale, slide 4192. All to same size, approx. $\times 60$.



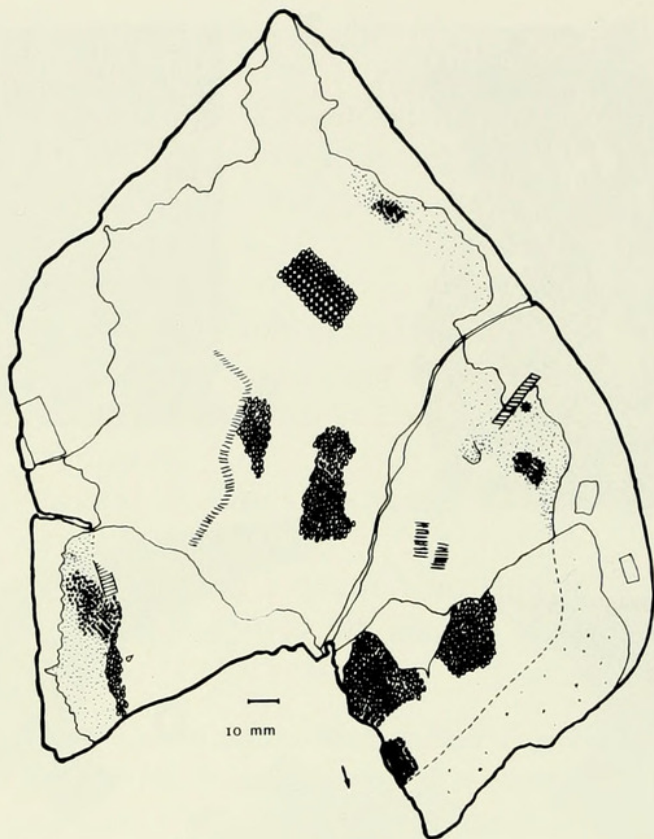


Figure 1. *Thelodus macintoshi* Stetson 1928 = *Thelodus parvidens* Agassiz 1838. Holotype, MCZ 2035. Close dotting: small *T. parvidens* scales in part, towards the sides of the heart-shaped nodule (probably the region of the pectoral fins). Larger scales in center; good articulated patches shown. Asterisk mark: one scale of *T. trilobatus*. Parallel bars: cracks in the nodule with slickensides. Clear rectangles: specimen labels. Arrow points to anterior.

RESULTS

Material. Examination of Stetson's specimens and his thin sections (to which the 1928 plates do not do justice), and of Denison's material, reveals that the material attributed to *T. macintoshi* is heterogeneous: it comprises at least two genera of thelodonts, and one specimen is actually an acanthodian. *T. macintoshi* (s.s.) is almost certainly synonymous with *T. parvidens*. I propose that *T. macintoshi* Stetson should be formally considered a junior synonym of *T. parvidens*, but I shall refer to *T. macintoshi* in an informal sense to distinguish the New Brunswick material from other material.

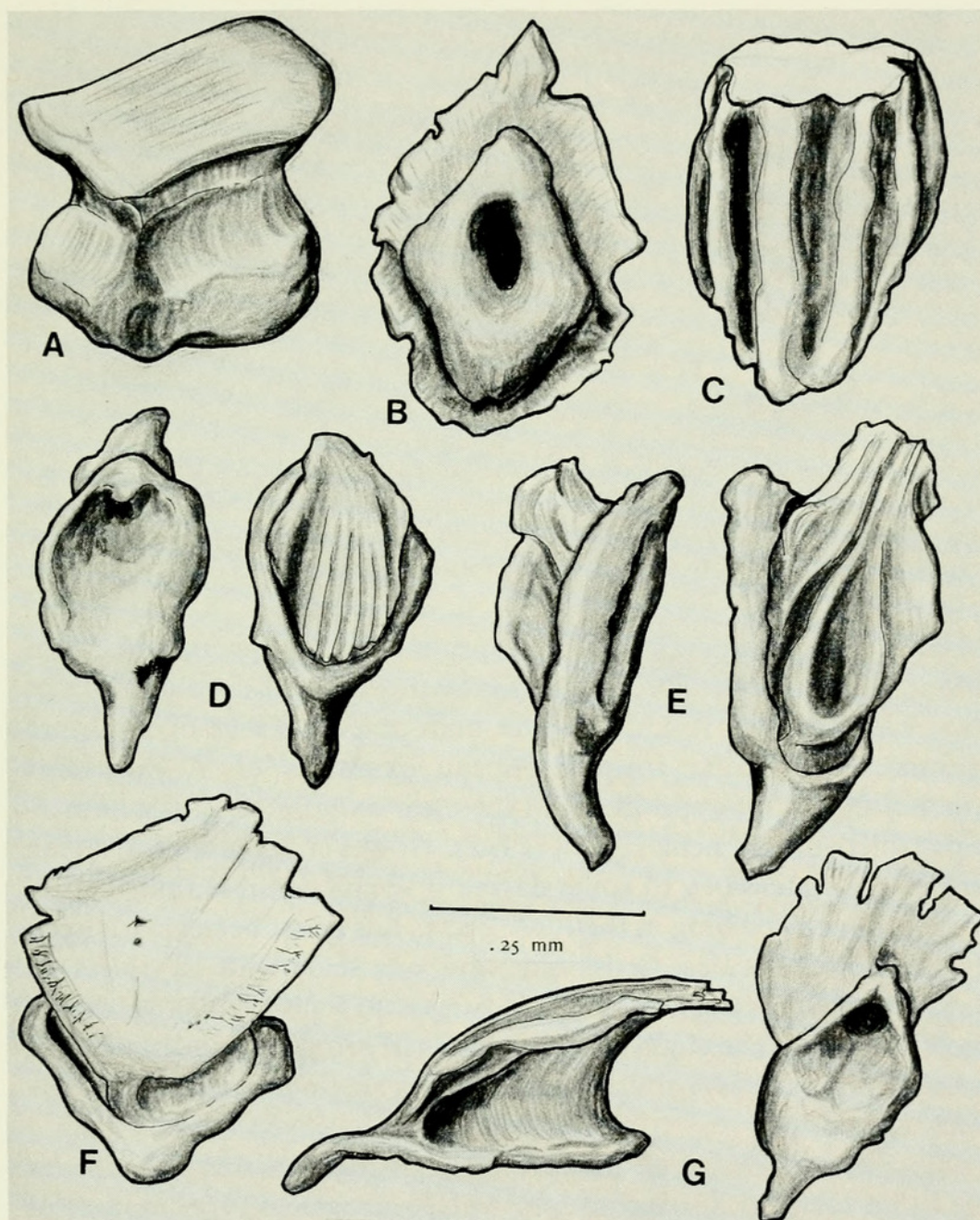


Figure 2. Isolated scales from nodule PF 9603 from horizon B of Denison, Cunningham's Brook, Nerepis, New Brunswick. A) *T. parvidens*, lateral view showing neck riblets, PF 9603.1; B) *T. parvidens*, ventral view, PF 9603.2; C) *T. bicos-tatus*, dorsal view of broken crown, PF 9603.3; D) *T. trilobatus*, ventral and dorsal views, PF 9603.4; E) *T. trilobatus*, lateral and dorsal views, PF 9603.5; F) *T. trilobatus*, dorsal view of smooth crown, PF 9603.6; G) *T. trilobatus*, lateral and ventral views, PF 9603.7.

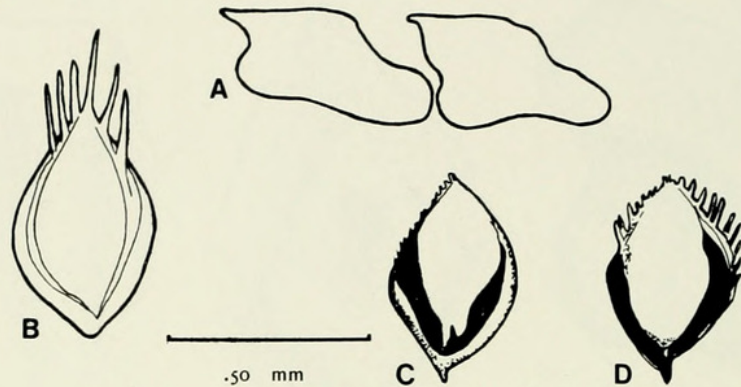


Figure 3. Scales on paratype of *T. macintoshi*, MCZ 2036. A) *Loganella* sp., two scales seen in cross section; B) *Loganella* sp., body scale in crown view showing unbroken posterolateral spinelets; C-D) *Loganella* sp., body scales in crown view with small anterior basal process and posterolateral neck spinelets.

The scales of the *T. macintoshi* specimens are large, up to 1.5 mm long, and in an advanced stage of growth with well-developed bases (see Fig. 2A, Pl. 1A-C); they are undoubtedly scales of a mature animal. They differ from European examples of *T. parvidens* (including the type specimen) in the clear expression of the numerous riblets on the neck region (Pl. 2). However, as most European scales are waterworn to some degree it seems possible that the full extent of neck ribbing in the type species has never been clearly seen in the isolated scales. Gross did show one scale with 12 riblets on one side of the neck (1967, Pl. 1, Fig. 3A) but their number is usually much smaller. The slight differences in rib ornament on the neck of scales may reflect local variation within a single population of *Thelodus parvidens*.

Furthermore, some of the specimens, including coprolitic masses and thin sections, show that scales of *T. bicostatus* type are part of the *T. parvidens* squamation (see Fig. 2). Despite the fact that the scales of *T. bicostatus* are very distinctive, both Gross (1967) and Turner (1973, 1976) thought they might be special scales of *T. parvidens*, while retaining the specific name *bicostatus*. One scale on the type specimen (MCZ 2035) appears to belong to *T. trilobatus* (see Fig. 1). A patch of small striated scales among the larger rhomboid *T. parvidens* scales on specimen BMNH P52444 could also belong to *T. trilobatus*. Scales of this species are also seen in coprolitic masses (Fig. 2D-G). Thin sections of scales from the nodules

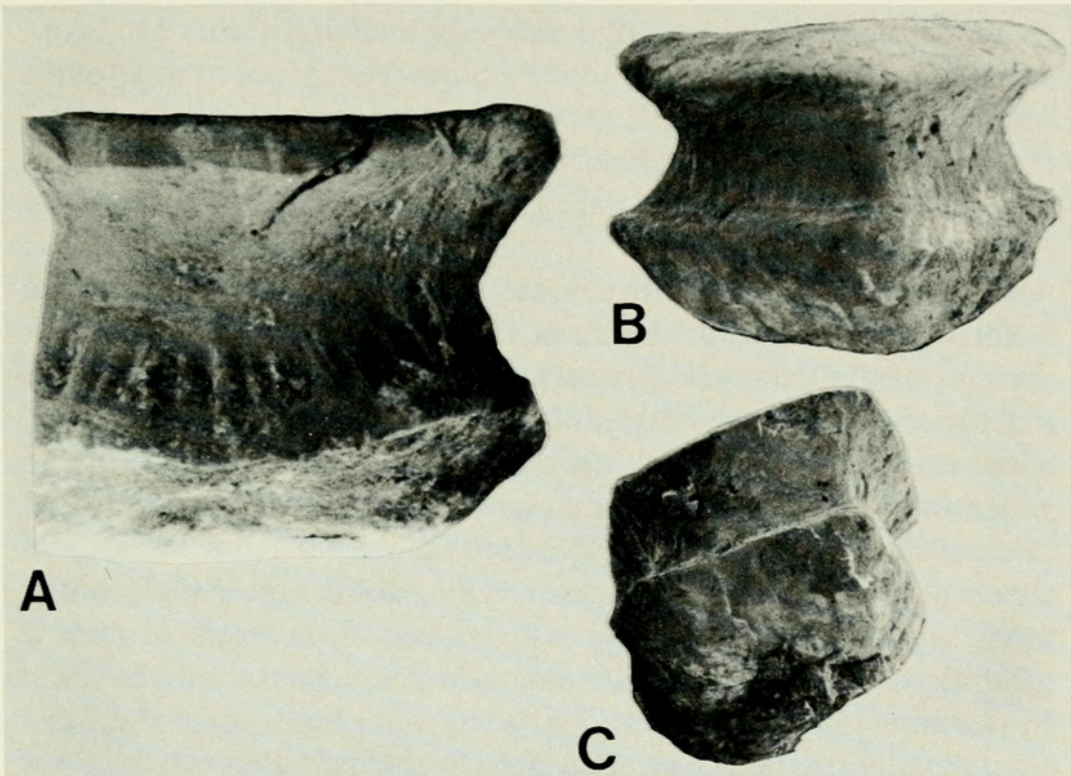


Plate 2. Scales of *Thelodus parvidens* from coprolitic nodule from Cunningham's Brook, Nerepis, New Brunswick. A) Detail of neck in lateral view showing riblets on lower neck, PF 9603.8, approx. $\times 60$; B) Scale in lateral view, PF 9603.8, approx. $\times 45$; C) Scale in posterobasal view showing pulp cavity, PF 9603.10, approx. $\times 45$.

confirm the presence of *T. parvidens* in association with *T. bicostatus* and *T. trilobatus* (see Pl. 1). Thus the *T. macintoshi* material confirms the synonymy of *T. parvidens*, *T. trilobatus* and *T. bicostatus* postulated initially by Gross (1967).

The most interesting discovery in this re-examination of Stetson's type material is the presence of at least one specimen of a loganiid. The paratype of *T. macintoshi* (MCZ 2036) is not a thelodontid, but a specimen of *Loganella* sp. cf. *L. ludlowiensis* (Gross 1967) or perhaps cf. *L. martinssoni* (Gross 1967). [The genus name *Logania* formerly attributed to this and other loganiid species is preoccupied (*Logania* Distant—Lepidoptera; Whitley 1976). Here I propose to use the replacement name *Loganella*.] The figures in Stetson's paper depicting scales with rim spines actually represent sagittal sections through *Loganella* scales (see Fig. 3). The scales in the nodule are sometimes broken through, exposing the slit-like pulp canal and

navicular shape of typical loganiid body scales (cf Gross 1967 e.g., Figs. 11 I-K).

At least two specimens from Nerepis, one in each of the collections at MCZ and the Field Museum, are not thelodonts but acanthodians. The scales are those of an ischnacanthid cf *Gomphonchus*.

It is not really difficult to see why Stetson did not recognise the different thelodonts in his fauna. Before 1928 only a few cross-sections of *Thelodus* scales, except those of *T. parvidens*, had been illustrated. Knowledge of the histological structure of scales did not become refined until the comprehensive study by Gross (1967), in which he separated the genus *Logania* from *Thelodus*. The MCZ houses the thin sections Stetson used; those cut from MCZ 2036 show the teardrop-shaped outlines of *Loganella* scales cut in horizontal section, with a slit-like pulp cavity. Nine slides of nodule pieces containing scales of *T. macintoshi* are housed at the Field Museum.

In the main, these scales are well-preserved and the sections show clearly that the scales belong to *T. parvidens*: some sections of the scales are mere "ghosts," the internal structure of the dentine having been recrystallised. One slide, PF slide 4187/52-102b, contains cross-sections of two scales of *T. bicostatus* (Hoppe 1931) (see Pl. 1E). Many of the scales of *T. parvidens*, including the *bicostatus* and *trilobatus* forms, exhibit clear incremental lines in the dentine; there are from nine to 11 in large scales and two to three in small scales (see Pl. 1). The incremental lines in thelodont scales are a measure of scale growth (Gross 1967). Whether the lines represent annual or seasonal increments may never be ascertained; if the animals were living in warm near-equatorial waters, as has been suggested for Siluro-Devonian vertebrates on other occasions (e.g., Halstead and Turner 1973), then it seems possible that the lines represent seasonal fluctuations in the availability of calcium and/or phosphate. Some scales are also penetrated by what look like fungal hyphae, similar to those described by Goujet and Locquin (1977) and Karatajute-Talimaa (1978) (see Pl. 1A, F).

Size of T. parvidens. Several of the nodules (e.g., those containing the holotype, see Fig. 1) contain articulated squamation which indicates that the thelodonts were very large. Stetson was correct in estimating that *T. macintoshi* was longer than *Turinia pagei* (Powrie

1870), the largest known thelodont at that time. He considered that some eight to ten inches would need to be added to the length of the holotype *Turinia*, making an estimate of 22 inches (around 550 mm) for *T. macintoshi*. Study of the type specimen shows that scales towards the center are very large, around 1.5 mm square, and closely packed in neat diagonal rows, whereas towards the antero-lateral margins the scales are progressively smaller, around 0.5 mm square and along the lateral margins the very small scales are much disrupted (Fig. 1). I suggest that, by comparison with the type specimen of *Turinia pagei* (see Turner 1982), the type specimen exhibits part of the cephalothorax extending to the region of the proximal tips of the pectoral fins. The specimen measures about 300 mm long by 250 mm wide. Given that the cephalothorax was probably about one quarter to one third of total body length, this New Brunswick thelodont might have had a length between 900 and 1200 mm. Other nodules in the collections examined show areas of squamation at least as large as that in the type specimen. With a length around one meter, these specimens of *T. parvidens* are the largest thelodonts found to date. This more than confirms Stetson's prediction about the size of the animals.

Age of the Nerepis fauna. Matthew (1888) considered the fish-bearing beds to be of Niagaran age because of the associated fauna, which includes *Ceratiocaris pusillis* and the xiphosuran *Bunodella horrida* (Denison 1956). Bailey and McInnes (1888) reported that Matthew regarded the beds to be about the same age as those containing *Palaeaspis* in the United States, that is, the Medina and Clinton Groups, and equivalent to Divisions 2 and 3 of the Anticosti Group and Groups B and B¹ of Arisaig. Westoll (1958a) placed the beds within the Wenlock, equivalent to the Lockport of the United States.

Both the Long Reach and Jones Creek Formation beds lie within the Mascarene Group, referred to as the Upper Silurian by the Canadian Geological Survey (MacKenzie 1964). When MacKenzie's maps were published in 1964 it was still not certain whether the Jones Creek Formation lay above, or below, the Long Reach Formation. The latter has been dated as Upper Llandovery/Lower Wenlock (C6), because of its *Costistricklandia-Eocoelia* community (Berry and Boucot 1970). MacKenzie (1951) had placed the Long Reach Formation above the Jones Creek Formation, but Berry and

Boucot, following a statement by MacKenzie, considered that it must rest below and that the Jones Creek Formation was of Ludlow/Pridoli age (see also Blieck 1982). McCutcheon (1981) has reiterated this interpretation, which would imply a large time gap between the two formations. I am not able to ascertain from the literature if this hiatus is discernible in the field. On their correlation chart Berry and Boucot (1970) show the Long Reach Formation extending from ?Upper Llandovery to Ludlow, but based on the brachiopod fauna, they prefer a Late Llandovery/Early Wenlock age. The Jones Creek Formation is possibly as old as Upper Ludlow (Ludfordian), for, as Berry and Boucot point out, the beds contain a *Salopina* community which is thought to signify Ludlow shallow water conditions in the Welsh Borderland (Lawson 1975).

Berry and Boucot compared the Jones Creek Formation with the Pembroke Formation of Maine. Devonian fish material has been discovered in the Eastport Formation of this region by Denison (Field Museum collections) but is not described yet. As the stratigraphy and structure of the Nerepis area seem complex, perhaps a more thorough search for fish remains in equivalent Siluro-Devonian beds nearby in Canada and in the United States would help clarify the succession.

The association of cyathaspids, acanthodians and *T. parvidens* (including *trilobatus* and *bicostatus* varieties) and a *Loganella* sp. cf. *L. ludlowiensis* in New Brunswick could be as old as early Wenlock and no younger than early Downton. A similar assemblage of these thelodont species and acanthodian scales has been found in sediments as old as Lower Wenlock in the Welsh Borderland (Turner 1973) and also in the Upper Llandovery of Norway (Turner 1984), and it is also found throughout the Upper Ludlow and early Downton of Europe (Turner 1973; Karatajute-Talimaa 1978; Märss 1982b). Märss (1982b) suggests that the pre-late Ludlow loganiid in the Welsh Borderland is in fact *L. martinssoni*. The possibility that the New Brunswick loganiid may belong to this latter species cannot be ruled out. Cyathaspids are known from supposed Upper Llandovery and Wenlock sequences in the Canadian Arctic but details of these early forms are not yet published (Denison 1964; Thorsteinsson 1967; Dineley and Loeffler 1976). In their review of cyathaspids Dineley and Loeffler (1976) compared *Cyathaspis acadica* with *C. banksi*, known from the Ludlow and early Downton of

the Welsh Borderland. It seems likely, however, following the reasoning of Elliott (1978) and of Dineley and Loeffler, that cyathaspids occur earlier in Canada than in Europe. More work on the Canadian cyathaspids might help clarify their relationships and biostratigraphic significance.

DISCUSSION

Implications. As I predicted (Turner 1970), *T. macintoshi* is very closely related if not identical to the type thelodont *T. parvidens*. Also the type material contains *T. bicostatus* and *T. trilobatus*. These three scale forms, *T. parvidens*, *T. bicostatus* and *T. trilobatus*, are elements of the Baltic-Anglo-East Canadian Silurian fauna (the *T. parvidens* assemblage of Turner 1973). This assemblage may represent a facies fauna indicative of the onset of "red bed" conditions.

If the thelodonts do come from the Long Reach Formation and the age of the fish beds is confirmed as early Wenlock, or even late Llandovery, this will add weight to the predicted occurrence of *T. parvidens* throughout the southern Laurasian region in the early Silurian. The appearance of *T. parvidens* before the late Wenlock is disputed by Karatajute-Talimaa (1978), who has not found it in any of the older localities which she has investigated. However, the fact that *T. parvidens* did appear in the late Llandovery is confirmed by its discovery in the Norwegian succession. If this is the oldest occurrence then there must have been the possibility of dispersal of *T. parvidens* between the west Baltic, the Welsh Borderland and New Brunswick. This would imply a shallow water connection between at least two of these three regions in mid-Silurian times.

The *T. parvidens* assemblage could also represent a cline, with the *T. macintoshi* form to the "west" of the range in New Brunswick, and forms such as *T. costatus* (Pander 1856), *T. sculptilis* Gross 1967, and *T. admirabilis* Märss 1982 to the "east" in the southern Baltic—even, perhaps, including *T. marginatus* Karatajute-Talimaa 1978. *T. trilobatus*, *T. bicostatus*, and *T. pugniformis* Gross 1967 would be included in *T. parvidens* as varieties because all possess a similar histological structure. These thelodonts would be placed within Blicek's Ichthyofacies IIA (Blicek 1982). Blicek (1982, Fig. 5) envisaged the New Brunswick site as located within the Appalachian channel with a possible link to the Welsh Borderland and elsewhere

in western Europe via a narrow shallow water passage. New Brunswick was almost certainly in connection with the Anglo-Welsh cuvette, Norway and probably elsewhere in the Baltic hinterland at some point during late Llandovery to early Downton times (see also Turner and Tarling 1982).

Scales of *T. parvidens* have also been found in the Ludlow Moydart Formation of Nova Scotia (Ørvig in Boucot *et al.* 1974) and those of "*Thelodus* sp." in the Upper Silurian (Lower Devonian?) Oriskany Sandstone of Nictaux Falls, Nova Scotia (Eastman 1907, Gardiner 1966). Thus there are indications that the *T. parvidens* fauna was quite widespread in eastern Canada by late Silurian times.

Environment. Denison (1956); Robertson (1957); and White (1958) considered that the fauna at Nerepis indicated a marginal marine or non-marine environment. From the state of preservation it would seem that the animals were living in or near a quiet backwater, possibly a supratidal pool or a lagoon. The style of preservation in the New Brunswick fish beds is virtually identical to that in the Lower Silurian fish beds of southern Scotland (see e.g., Ritchie 1968). At Lesmahagow and Hagshaw thelodonts, anaspids, ceratocarids, eurypterids and rare xiphosurans are found, often contained in nodules (considered to be coprolitic) within black shales. Some near-complete thelodonts are preserved in large nodules, and numerous scales occur in the center of nodules, probably the remains of consumed thelodonts. At Cunningham's Brook these coprolitic masses seem to be confined to one horizon (Denison's horizon B). There is little or no evidence of transport seen on any of the specimens; thelodont scales are not noticeably waterworn and a range of scale size is seen in the disarticulated scale masses in nodules as well as in articulated squamation (see Figs. 1, 2).

Denison (1964) discussed the state of preservation of the cyathaspids and found that one specimen, also found in a coprolite, was a juvenile on the evidence of its thin plates and scales. This also suggests that the fish were living and dying in a low-energy environment.

The large size of the thelodonts in the Nerepis fauna suggests that this was an ideal environment for these creatures which until now have invariably been thought of as small insignificant agnathans.

The thelodonts in the Lower Silurian of Scotland, belonging to *Loganella scotica* Traquair 1898, which seem to have lived in a similar environment, also exhibit a range of size from a few centimeters (juveniles) to quite large individuals (up to an estimated 400 mm). If similarity of faunal components and style of preservation are taken into account then the Nerepis site and Scottish lower fish beds could be of equivalent age, which would be late Llandovery to early Wenlock (e.g., Rolfe 1973).

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