LARGE TRISTICHOPTERIDAE (SARCOPTERYGII, TETRAPODOMORPHA) FROM THE LATE FAMENNIAN EVIEUX FORMATION OF BELGIUM

by GAËL CLEMENT

ABSTRACT. Remains of two large sarcopterygians are described from Famennian deposits in Belgium. One of them is referred to *Eusthenodon wängsjöi* Jarvik; it is the first occurrence of this genus in Belgium. The other, much larger one, appears to be a tristichopterid. It has a postspiracular; size and shape of the mandible similar to those of *Platycephalichthys skuenicus* and *P. bischoffi*; snout and cheek patterns close to those of *Eusthenodon*; unusual shape of the supratemporal resembling that of *Hyneria*, *Mandageria* and *Platycephalichthys skuenicus*; and tooth histology quite similar to that of *Eusthenodon* and *Platycephalichthys*.

KEY WORDS: Late Devonian, Belgium, Tristichopteridae, *Eusthenodon*, anatomy.

THE Tristichopteridae Cope 1889 (a senior synonym of Eusthenopteridae Berg 1940) is a group of advanced 'Osteolepiformes' (Ahlberg and Johanson, 1998), known from the Middle and Late Devonian (Late Givetian–Late Famennian). They occur in Scotland (*Tristichopterus* Egerton, 1861); Canada, the Baltic Region and Russia (*Eusthenopteron* Whiteaves, 1881; *Eusthenodon* Jarvik, 1952, according to Alekseev *et al*. 1994; *Platycephalichthys* Vorobyeva, 1959; and *Jarvikina* Vorobyeva, 1977); Greenland (*Eusthenodon* Jarvik, 1952; *Spodichthys* Jarvik, 1985); Pennsylvania, USA (*Hyneria* Thomson, 1968); Australia (*Mandageria* Johanson and Ahlberg, 1997; *Cabonnichthys* Ahlberg and Johanson, 1997; and *Eusthenodon*; Young 1993, Ahlberg *et al.* 2001); Morocco ('Eusthenopteridae' gen. et sp.? indet., Lehman 1977; Lelièvre and Janvier 1986); South Africa (*Eusthenodon*; Gess and Hiller 1995, Anderson *et al*. 1999); and Antarctica (*Notorhizodon*; Johanson and Ahlberg in press).

The first occurrence of large and partly articulated tristichopterids in the Devonian of Belgium is reported here. Previous findings of tristichopterid remains in Belgium and northern France are extremely scarce. Cloutier and Candilier (1995) pointed out that the two scales referred to the porolepiform *Glyptolepis benedeni* by Lohest (1888, pl. 9, figs 4–5) from the Famennian of Belgium (Evieux Formation, Strud and Modane) almost certainly belong to a tristichopterid (either *Eusthenopteron* or *Eusthenodon*). In addition, some ichthyoliths from the Lower Frasnian (Beaulieu Formation, Cambresèque Member) of Pas-de-Calais, France, have been tentatively referred to ?*Spodichthys* sp. by Derycke *et al*. (1995).

MATERIAL AND METHODS

The material described herein comes from a large, isolated dolomitic sandstone (dolostone) block bearing scattered scales, lepidotrichia and dermal bones of two large species of Tristichopteridae. It was discovered by Dr Eddy Poty (Liège University, Belgium) in 1985. Some of these elements are overlain by large scales of the porolepiform *Holoptychius*. Because of the extreme hardness of the dolostone, most elements have been prepared by removing the bone with hydrochloric acid in order to obtain a natural mould from which an elastomer cast could be made.

Only the left mandible of the larger species and the parieto-ethmoidal portion of the skull roof of the smaller one, which were already partly exposed on the somewhat weathered surface of the slab, have been mechanically prepared with an engraver and needles.

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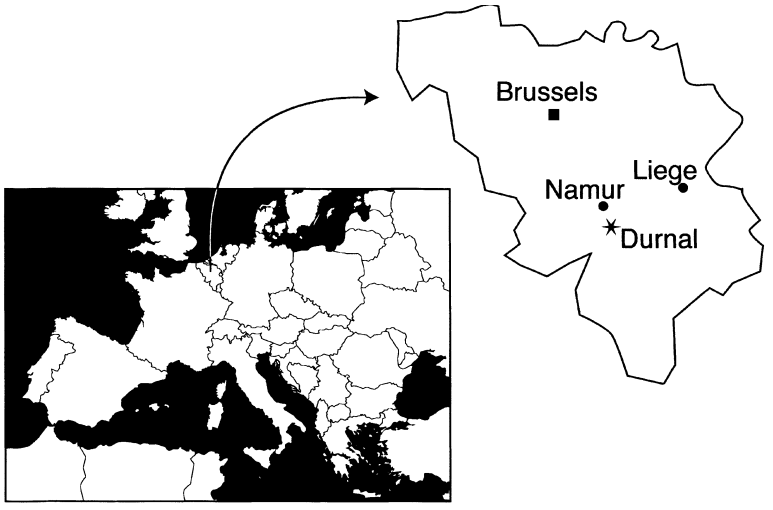


TEXT-FIG. 1. Map showing the location of the Langlier quarry, near Durnal, Namur Province, Belgium.

The material belongs to the collection of the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, and is registered with the acronym MNHN ARD.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The material was discovered in an isolated block from the Langlier quarry, 1·5 km north of Dorinne and 2 km south of Durnal, along the Bocq valley, Namur Province, Belgium (Text-fig. 1). This quarry is situated in the eastern part of the Dinant synclinorium, south of the London-Brabant Massif in an outcrop of the Evieux Formation of the upper Famennian 'Condroz Sandstones' sequence. According to Goemaere (1995), the Evieux Formation is characterised by an alternation of micaceous arkoses and siltstones, dolostones, and anhydrites, which suggests a mixed alluvio-lagoonal environment with estuarine or tidal delta influences.

During the Devonian, the Condroz Shelf was located between latitudes 20 and 30° South, where it was presumably subjected to westerly tropical winds and storms. Consequently, the climatic conditions were analogous to those of the present-day Sahel; that is, relatively arid to semi-arid. Dolostones apparently resulted from direct physico-chemical precipitation in lagoonal ponds (Thorez, 1969).

SYSTEMATIC PALAEONTOLOGY

Class SARCOPTERYGII Romer, 1955
Order OSTEOLEPIFORMES Berg, 1937
Family TRISTICHOPTERIDAE Cope, 1889

Genus EUSTHENODON Jarvik, 1952

Remarks. Apart from this material, *Eusthenodon* remains were previously recorded from the Famennian of central Russia (Andreyevka-2 locality in the Tula Region; Alekseev *et al.* 1994), Australia (Eden, New South Wales; Ahlberg *et al*. in press, and Grenfell, New South Wales; Young 1993), and South Africa (Witpoort Formation; Gess and Hiller 1995; Anderson *et al.* 1999). However, none of the Russian, Australian and South African specimens has yet been described in detail. Therefore, the diagnosis of the genus *Eusthenodon* rests essentially on the type species.

Eusthenodon wängsjöi Jarvik, 1952

Text-figures 2–4

Diagnosis (emended from Jarvik 1952). Large tristichopterid approximately 2·5 m in length. It differs from other known tristichopterids by the following combination of characters: a broad snout; pineal bones tear-drop-shaped and situated well posterior to orbits; posterior process of posterior supraorbital much longer than orbital margin; lateral extrascapulars well separated in the midline anteriorly; maxilla attains its greatest height in the anterior part of the bone, close behind its centre of radiation; presence of dentary fang pair and enlarged tooth at anterior end of premaxilla; ornamentation consisting of ridges forming distinct networks, whereas independent tubercles are rare.

Remarks. The Tristichopteridae is a clade uniquely defined by the presence of a postspiracular bone (Jarvik 1980; Cloutier and Ahlberg 1996). *Eusthenodon wängsjöi* resembles *Mandageria* in various derived characters (e.g. in having the jugal and postorbital excluded from the orbital margin by the contact between the lacrimal and the posterior supraorbital and in lacking a contact between the intertemporal and posterior supraorbital). It differs in the absence of fusion of the supratemporal, tabular and postparietals bones, in the lateral extrascapulars being widely separated in the midline anteriorly, and in having proportionately larger scales (Johanson and Ahlberg 1997).

Material. The elements referred to this species are part of the parieto-ethmoidal skull roof, a left anterior supraorbital, parts of the right lacrimal, the maxilla, the infradentaries and dermopalatine of the left side, and a complete subopercular of the right side, along with numerous lepidotrichia and scales.

Description

Skull roof (Text-figs 2A, 3B). The parieto-ethmoidal shield is elongated in overall shape and its proportions are identical to those of the East Greenland material of *E. wängsjöi*. The ornamentation consists of a coarse network of anastomosing ridges and tubercles that is also quite similar to that of the Greenland material.

The nasal series (Na, Text-fig. 3B) is incomplete. Two nasals are clearly visible on the right side, the posterior one being considerably expanded anteriorly. On the left side, the posteriormost two nasals are present; the posterior one is large and rounded in shape, whereas the anterior one is small, with a short posterior edge.

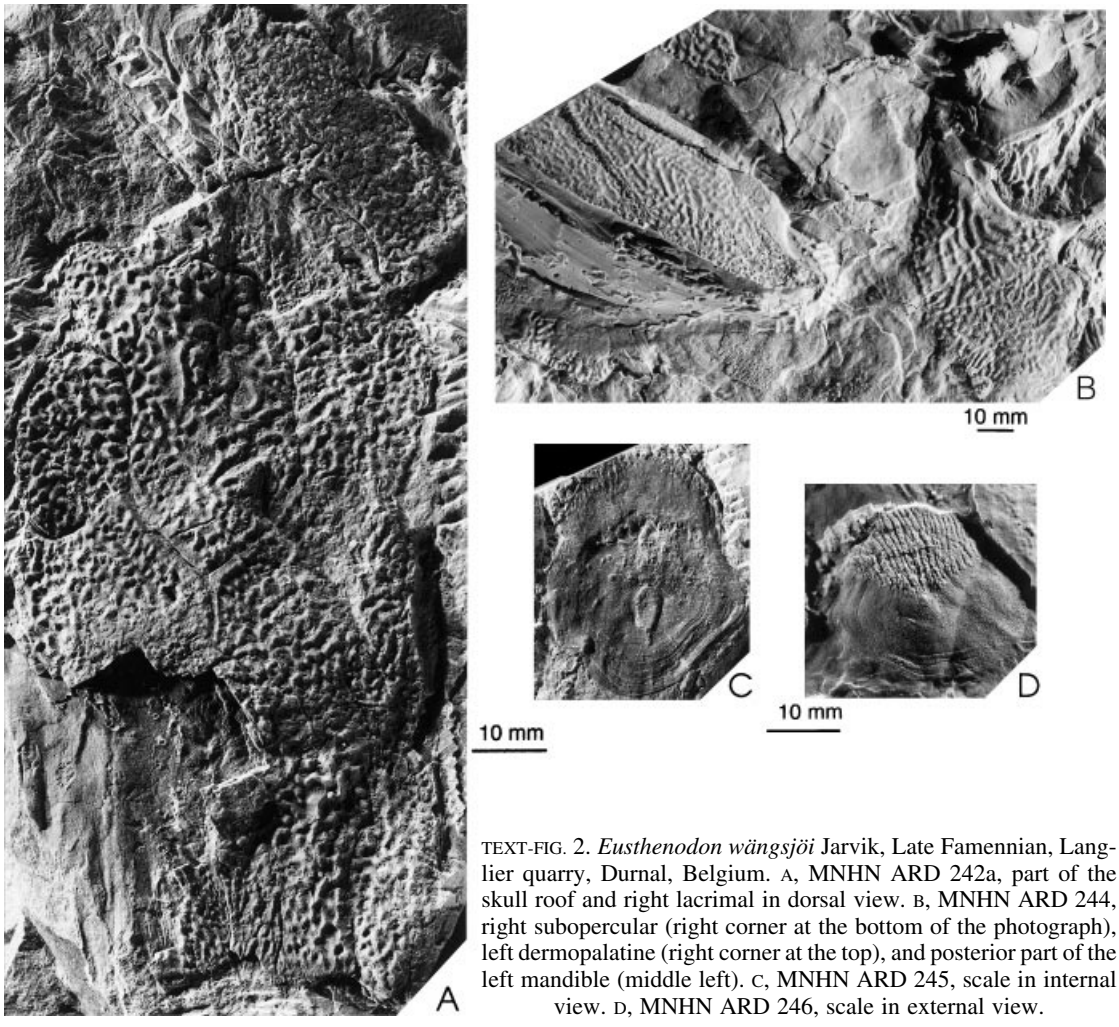
The shape and ornamentation of the posterior median postrostral (Mpr, Text-fig. 3B) and the parietals (Pa, Text-fig. 3B) are similar to those of the *Eusthenodon* material from Greenland. Unfortunately, the parietal of the left side is damaged and the precise shape of the pineal plates (pin.pl, Text-fig. 3B) and foramen cannot be inferred. Nevertheless the pineal fenestra distinctly ends posteriorly near the posterior margin of the parieto-ethmoidal shield (pm.Pa, Text-fig. 3B). The anterior extremity of the intertemporal (It, Text-fig. 3B) and the posterior edge of the overlap area for the supraorbital (od.So, Text-fig. 3B) are slightly damaged but it seems that the parietal could have been in contact with the postorbital, as in *Mandageria* (Johanson and Ahlberg 1997, fig. 21) and *Eusthenodon* (Jarvik 1952, fig. 26B). An isolated anterior supraorbital of the left side (Text-fig. 3A) lies close to the parieto-ethmoidal shield. Its shape is less elongated than in the Greenland *Eusthenodon* material, and quite similar to that in *Eusthenopteron*, although its anterolateral margin contacting with the lacrimal is more concave (od.La, Text-fig. 3A).

Maxilla, lacrimal and subopercular (Text-figs 2B, 3B, D). Part of the maxilla, visible in internal aspect, and the lacrimal (La, Text-fig. 3B) of the right side are similar in shape and size to those of *E. wängsjöi* from Greenland, although the lacrimal is slightly more elongated in the Belgian material. This, along with the slightly different shape of the anterior supraorbital, would be the only possible difference, considering the available material, between this Belgian and the Greenland species.

It is worth noting that, contrary to most other ‘osteolepiforms’, the maxilla shows a thin area overlapped by squamosal. This character was regarded by Jarvik (1985) as unique to *Eusthenodon*, but it seems that *Platycephalichthys bischoffi* also presents this feature (Vorobyeva, 1962, pl. 14, fig. 2; fig. 12).

The subopercular of the right side (Sob, Text-figs 2B, 3D) shows a coarse ornamentation, a large overlap area for the lower jaw (od.Lj, Text-fig. 3D) and another smaller one for the opercular (od.Op, Text-fig. 3D).

Palate: dermopalatine (Text-figs 2B, 3E). The dermopalatine of the left side is almost complete and extends slightly forwards lateral to the fenestra exochoanalis (fe.exch.n, Text-fig. 3E). There is no marginal tooth row in front of the fangs, as in *Mandageria fairfaxi* (Johanson and Ahlberg, 1997), and unlike *Eusthenopteron*. This feature could be

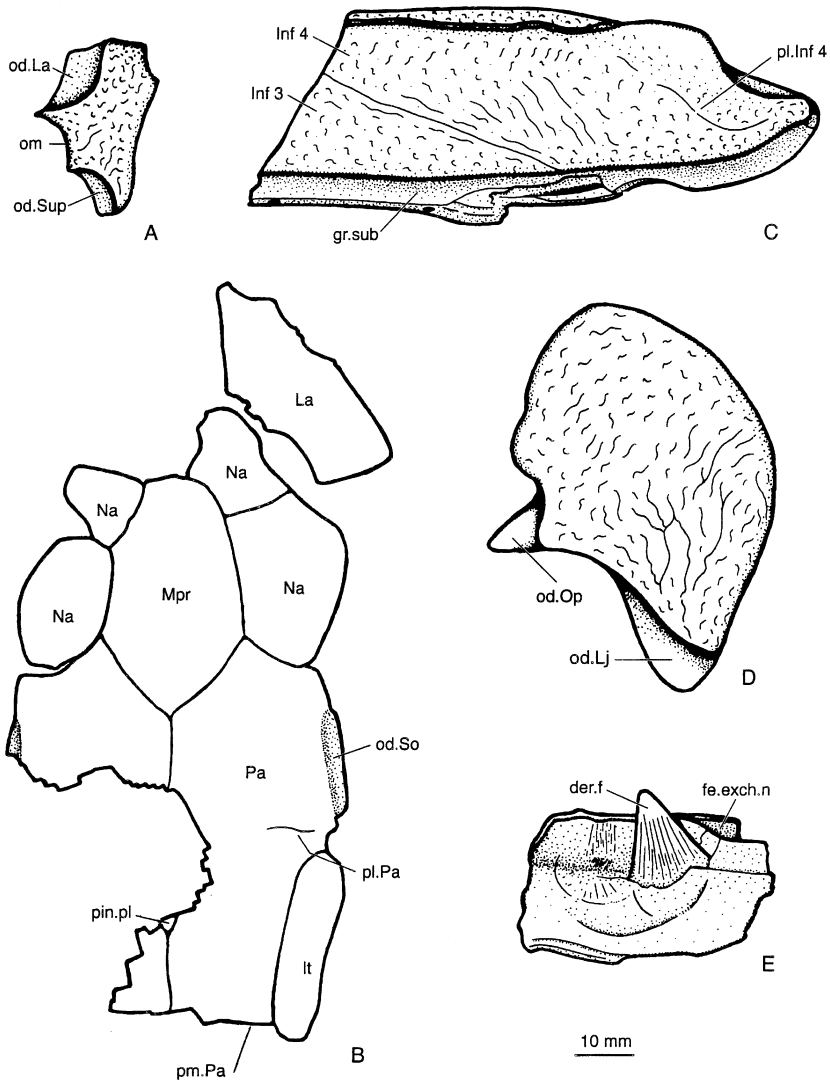


TEXT-FIG. 2. *Eusthenodon wängsjöi* Jarvik, Late Famennian, Langlier quarry, Durnal, Belgium. A, MNHN ARD 242a, part of the skull roof and right lacrimal in dorsal view. B, MNHN ARD 244, right subopercular (right corner at the bottom of the photograph), left dermopalatine (right corner at the top), and posterior part of the left mandible (middle left). C, MNHN ARD 245, scale in internal view. D, MNHN ARD 246, scale in external view.

compared to the coronoid condition in, on the one hand, *Cabonnichthys*, *Eusthenodon*, and *Mandageria* (i.e. no marginal coronoid teeth, except on the posterior part of the posterior coronoid) and, on the other hand, *Eusthenopteron* (i.e. presence of marginal teeth all along the coronoid). The dermopalatine supports a pair of fangs (der.f, Text-fig. 3E), the anterior one being situated just behind the choana, as in *Eusthenopteron*, but contrary to *Cabonnichthys burnsi* (Ahlberg and Johanson, 1997) and *Mandageria*. Furthermore, the dermopalatine of the latter two species is more elongated than those of *Eusthenopteron* and *E. wängsjöi*, and this may be linked to the elongation of the entire snout in these Australian species. The fang is large and straight, laterally compressed, and bears longitudinal grooves on the middle part of its surface.

Mandible (Text-figs 2B, 3C). The infradentary 4 (Inf4, Text-fig. 3C) and the posterior part of the infradentary 3 (Inf3, Text-fig. 3C) of the left side are preserved. Infradentary 4 shows the infradentary pit-line (pl.Inf4, Text-fig. 3C) and the characteristic hook shape of its posterior end. The deep groove for the submandibular bones (gr.sub, Text-fig. 3C) is also visible.

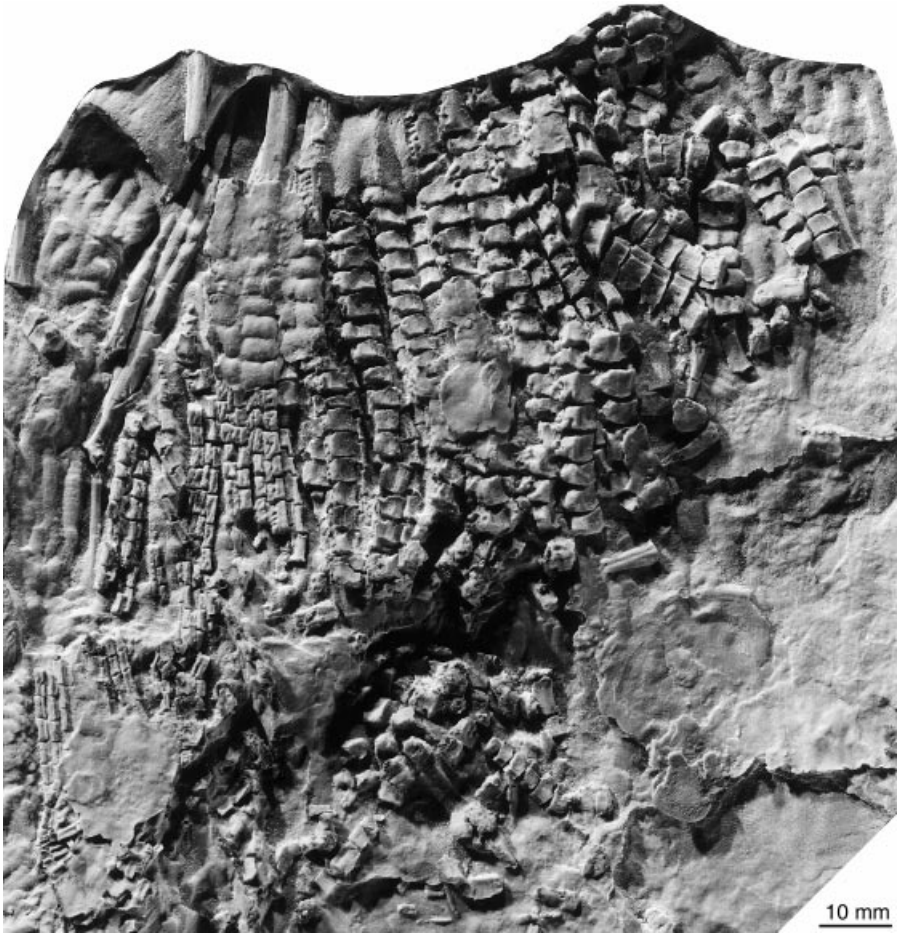
Scales (Text-fig. 2C–D). The scales are *Eusthenopteron*-like but their overlap area is larger than in *Eusthenopteron* and the ornamentation of their uncovered surface consists of interconnected, sinuous ridges. Their internal surface shows the characteristic drop-shaped knob.



TEXT-FIG. 3. *Eusthenodon wängsjöi* Jarvik, Late Famennian, Langlier quarry, Durnal, Belgium. A, MNHN ARD 242b, left anterior supraorbital. B, MNHN ARD 242a, part of the parieto-ethmoidal division of the skull roof. C, MNHN ARD 244c, posterior part of the mandible. D, MNHN ARD 244a, right subopercular. E, MNHN ARD 244b, left dermopalatine.

Fins (Text-fig. 4). The appendicular skeleton is only represented by the distal portion of a fin with dermal fin rays and some large, partly preserved radials. The distal, jointed portion of the unsegmented rays is occasionally branched in the anterior part of the fin web, and consists of small, rectangular lepidotrichia that decrease in size distally.

Remarks. The smallest of the two tristichopterid species of this assemblage is referred to the genus *Eusthenodon* and, despite the incompleteness of the material, seems to be indistinguishable from the type species, *E. wängsjöi*, from the Famennian *Remigolepis*-series of Gauss Halvø and Ymer Ø, East Greenland (Jarvik 1952).



TEXT-FIG. 4. *Eusthenodon wängsjöi* Jarvik, Late Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 243, distal part of the pectoral fin.

TRISTICHOPTERIDAE gen. et sp. indet.

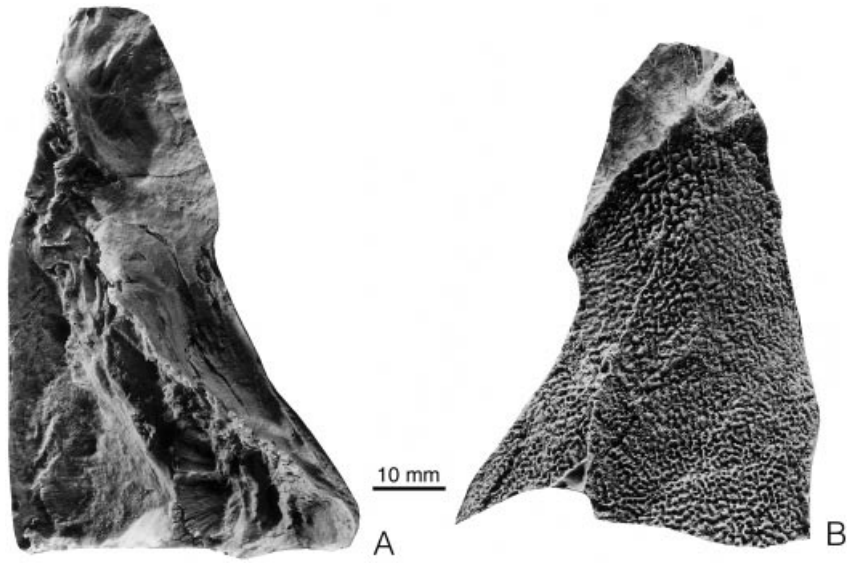
Text-figures 5–13

Description

The dermal bones of this second, very large fish are readily distinguished from those of *Eusthenodon wängsjöi* by their much finer ornamentation. The material referred to this form consits of a supratemporal, fused to part of the tabular, an opercular of the right side, a postspiracular and lateral extrascapular, part of the snout, part of the cheek, the mandible of the left side, and the ventral, distal part of the clavicle. Except for the clavicle, which is ornamented with a coarse ridge network, the ornamentation consists of a very fine ridge network.

Supratemporal and tabular (Text-figs 5A–B, 6A–B). The supratemporal (Su, Text-fig. 6A) and part of the tabular (Ta, Text-fig. 6A) of the left side are preserved in external and internal view. These two bones are fused together, but their suture, which is partly visible on the internal surface, is strongly interdigitated instead of being straight, as is the case in most of 'osteolepiforms'. The extratemporal seems to be lacking.

A large anterior overlap area for the intertemporal (od.It, Text-fig. 6B) and the postorbital (od.Po, Text-fig. 6B) projects anteriorly from the anterolateral part of the supratemporal. It is developed as in *Eusthenopteron* (Jarvik 1944,



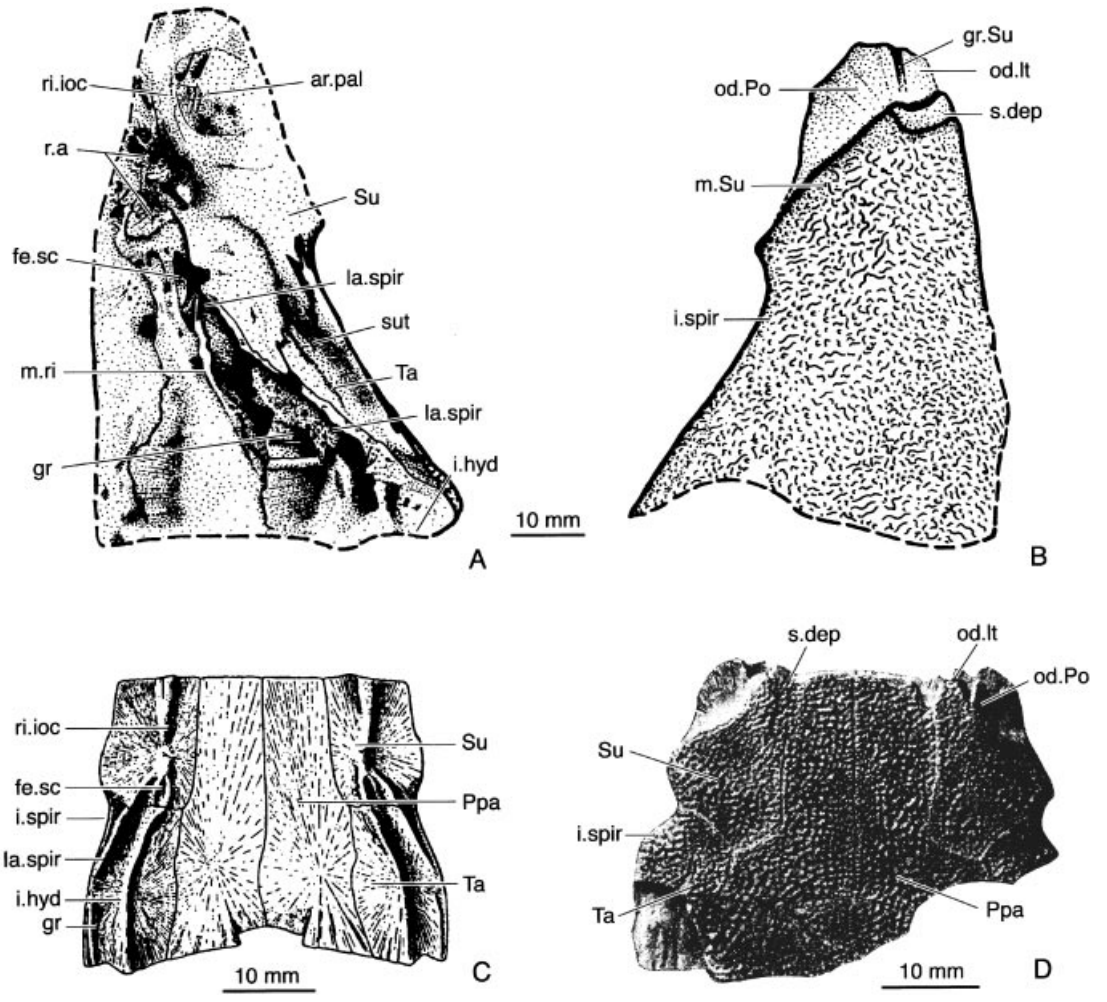
TEXT-FIG. 5. A–B, Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 248, left supratemporal and part of the tabular in ventral (A) and dorsal (B) views.

fig. 19C), *Megalichthys* (Bjerring 1972, fig. 1A) and *Notorhizodon* (Young *et al*. 1992, fig. 22C). A well-marked groove (gr.Su, Text-fig. 6B) is visible on the medial side of the overlap area for the intertemporal. Referring to Jarvik (1944), Young *et al*. (1992) argued that the ridge of the intertemporal can be fitted into the supratemporal groove and assumed that such a complex overlapping device made the intracranial joint immovable. A small depression (s.dep, Text-fig. 6B) is situated at the anterior end of the supratemporal, as in *Eusthenopteron* and *Eusthenodon.* According to Jarvik (1954, fig. 5B), this depression is overlapped by a dorsomedial lamina of the intertemporal. According to Bjerring (1967, p. 244, fig. 14C), this well-developed depression very likely served as the attachment for the stronger, marginal parts of the supracerebral ligament of the intracranial juncture apparatus; that is a median, elastic ligament that connected the supratemporals and the parieto-intertemporals.

The anterior margin of the supratemporal (m.Su, Text-fig. 6B), anterior to the spiracular notch (i.spir, Text-fig. 6B), is straight and oblique, contrary to the concave margin of the anterolateral expansion of the supratemporal in most of the Osteolepididae and Tristichopteridae (Text-fig. 6D), and in *Panderichthys*. However, a similar shape occurs the tristichopterids *Hyneria lindae* (Thomson 1968, according to the reconstruction in fig. 1), *Mandageria fairfaxi* (Johanson and Ahlberg 1997, fig. 10A, C) and *Platycephalichthys skuenicus* (Vorobyeva 1977, pl. 14, figs 1–2).

Contrary to all other Tetrapodomorpha, the distance between the anterior end of the spiracular notch and the posterior margin of the overlap area for the postorbital is very short (i. spir, od. Po, Text-fig. 6B). In addition, the supratemporal is very short, by comparison with the size of the other dermal bones referred to the same form. This suggests that the postparietal shield was short, relative to the cheek (Text-fig. 8A–B) and, thus, to the parieto-ethmoidal shield. According to Long (1985), the progressive lengthening of the parieto-ethmoidal shield, relative to the postparietal shield, is characteristic of the advanced Tristichopteridae. From the spiracular notch (i.spir, Text-fig. 6B), along the margin of the tabular and supratemporal, it may be inferred that the spiracular fenestra was very elongated in shape, by comparison with that of the other 'osteolepiforms'. None of the external openings of the lateral-line canal system described in certain 'osteolepiforms' (e.g. the Carboniferous genus *Megalichthys*) could be observed.

The ventral surface of the supratemporal displays a rough area that extends along the medial margin of the bone (r.a, Text-fig. 6A) and corresponds to the areas where the supratemporal was in contact with the underlying braincase. Anterior to this rough area, a ridge (ri.ioc, Text-fig. 6A) may have housed the infraorbital sensory canal. Lateral to the rough area a large and smooth depression (ar.pal, Text-fig. 6A) occurs, which housed the upper margin (paratemporal process) of the palatoquadrate. This depression is bounded off posteriorly by a prominent, ventromedially projecting lamina (la.spir, Text-fig. 6A). Passing through the internal surface of the tabular, this lamina decreases in size postero-laterally. Thomson (1968) suggested that the internal ridge of the supratemporal and tabular may have served as an anchoring device, preventing relative movements of the dermal skull roof and braincase.

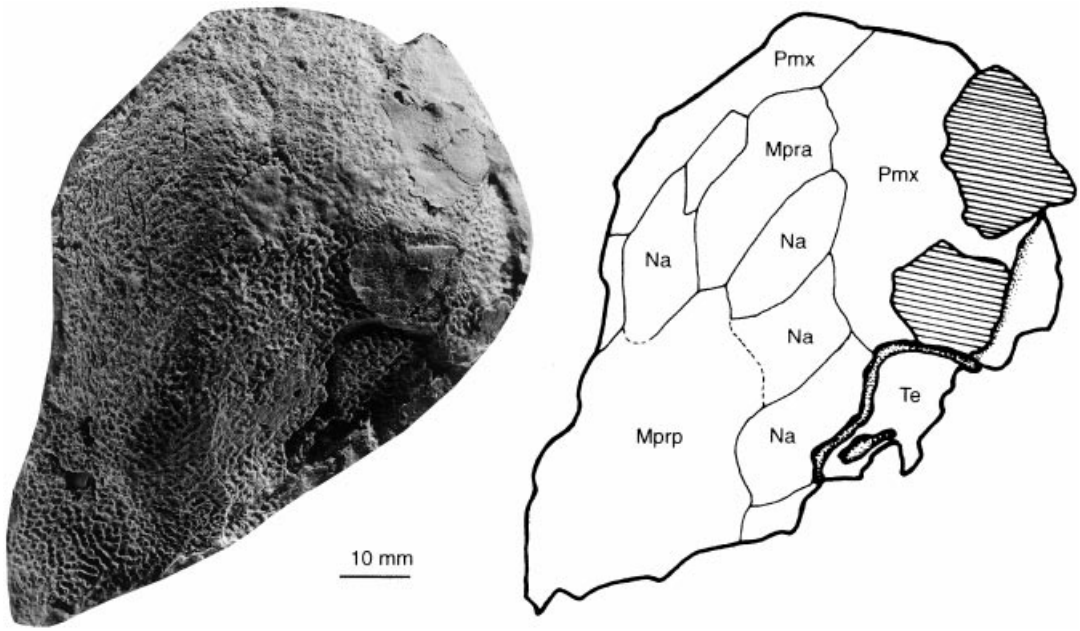


TEXT-FIG. 6. A–B, Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 248, left supratemporal and anterior part of the tabular in ventral (A) and dorsal (B) views. C, *Eusthenopteron foordi* Whiteaves, Frasnian of Miguasha, Quebec, Canada; postparietal shield in ventral view (from Jarvik 1954, labelling modified). D, *Eusthenopteron sävesöderberghi* Jarvik, Frasnian, western Russia and Latvia; postparietal shield in dorsal view (from Jarvik 1944, labelling modified).

Medially and parallel to this lamina, there is a second, prominent ridge (m. ri, Text-fig. 6A). These two ridges delimit a groove (gr, Text-fig. 6A) for a ridge-like part of the otoccipital bounding the fossa bridgei laterally and for the dorsal articular area for hyomandibular (i.hyd, Text-fig. 6A).

Snout (Text-fig. 7). The specimen shows two large premaxillae (Pmx, Text-fig. 7), almost complete nasal series (Na, Text-fig. 7), the anterior median postrostral (Mpra, Text-fig. 7), and the anterior part of the posterior median postrostral (Mprp, Text-fig. 7). The pattern of the anterior bones of the snout is quite similar to that of *Eusthenodon wängsjöi* (Jarvik 1952, fig. 23B, E), although the anteriormost nasal and anterior median postrostral are more elongated in shape than in the latter.

Extrascapulars (Text-figs 8A, 9A). The lateral extrascapular (Ext, Text-fig. 9A) of the right side is almost in connection with the opercular (Op, Text-fig. 9A) and the squamosal (Sq, Text-fig. 9A) of the same side. The lateral



TEXT-FIG. 7. Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 247, snout in dorsal view.

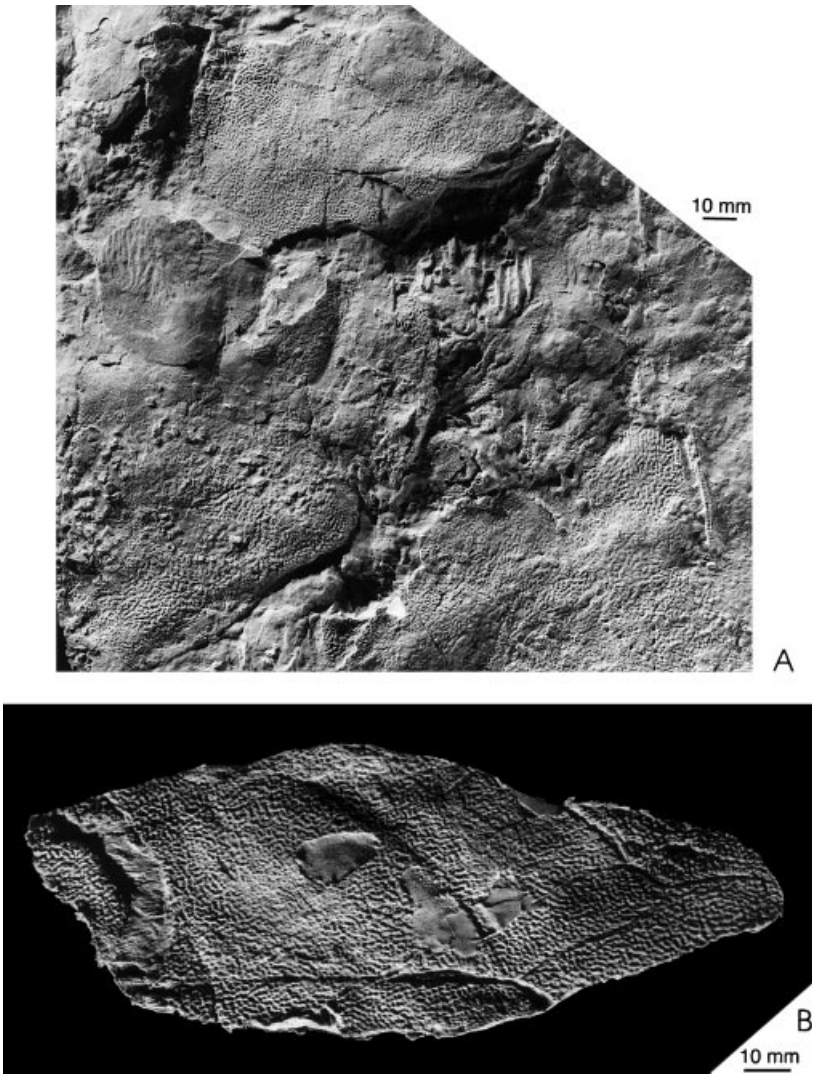
extrascapular shows an overlap area for the squamosal (od.Sq, Text-fig. 9A) in its anterolateral corner (as in *Eusthenodon*; Jarvik 1952, pl. 9). The postspiracular is not preserved in this material. It is a small bone, characteristic of the Tristichopteridae, and lodged between the opercular and the lateral extrascapular. It is not preserved here but when the outlines of the opercular, lateral extrascapular, and squamosal are all connected together, there remains a small crescent-shaped space between them; this suggests that a postspiracular was present. Furthermore, a small overlap area, presumably for the postspiracular (od.Pos, Text-fig. 9A), is present along the ventral margin of the extrascapular.

Cheek (Text-figs 8A–B, 9A–B). Part of the cheek of the left side is preserved and clearly shows the ventral part of the squamosal (Sq, Text-fig. 9B) and the adjacent bones. One remarkable detail is the overlap of the maxilla (Ma, Text-fig. 9B) by the squamosal (od.Sq, Text-fig. 9B), as in *Eusthenodon*, and possibly *Platycephalichthys bischoffi*, and contrary to all other 'osteolepiforms' (Jarvik 1985). The area of the quadratojugal overlapped by the maxilla (od.Ma, Text-fig. 9B) is visible along the posterodorsal margin of the maxilla. The shape of this area is the same as in *Eusthenodon wängsjöi* (Jarvik 1952, fig. 28).

The cheek pattern often shows a great variation within the same tristichopterid species (e.g. *Eusthenodon wangsjöi*; Jarvik, 1952) and, although the sutures between the squamosal and the quadratojugal (Qj, Text-fig. 9B) and between the squamosal and the jugal (Ju, Text-fig. 9B) are generally straight and strongly curved, respectively, these characters are highly variable. The dorsal parts of the squamosal and preopercular (Pop, Text-fig. 9A) of the right side are preserved in association with the extrascapular described above (Text-figs 8A, 9A).

Opercular series (Text-figs 8A, 9A). The opercular (Op, Text-fig. 9A) of the right side is almost complete and displays nearly the same ornamentation as the other dermal bones, yet turning into long, parallel ridges in its posterior part, as in *Hyneria*, *Mandageria* and *Cabonnichthys*, but unlike *Eusthenodon*. Its anterolateral corner forms a right angle and it shows an anterior area overlapped by the preopercular (od.Pop, Text-fig. 9A). There is no evidence for an area possibly overlapped by the postspiracular, as described in *Eusthenopteron* (Jarvik 1944, Fig. 9C) and *Eusthenodon* (Jarvik 1952, pl. 12, fig. 2).

Entopterygoid (Text-fig. 11A). Dorsal to the internal surface of the mandible is a small part of the right entopterygoid (enpt, Text-fig. 11A). It is covered with a shagreen of minute denticles and shows an oblique ridge (enpt.ri, Text-fig.

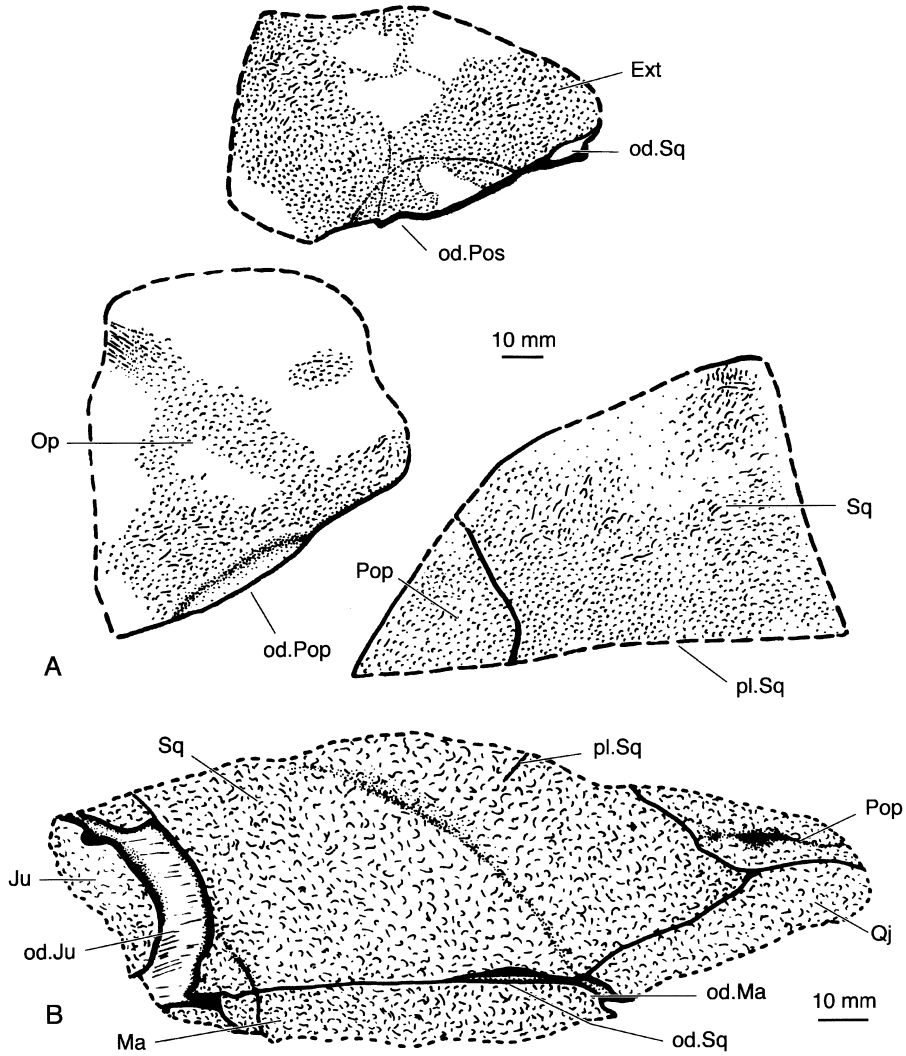


TEXT-FIG. 8. A–B, Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium. A, MNHN ARD 249, associated dorsal part of the right squamosal and preopercular (bottom right), part of the right opercular (bottom left), and extrascapular (top). B, MNHN ARD 250, posteroventral part of the left cheek.

11A). This ridge is present on the entopterygoid of most 'rhipidistians' *sensu* Panchen and Smithson (1987) and is especially sharp in tetrapodomorphs, as here.

Mandible (Text-figs 10, 11A–B). The mandible of the left side is approximately 370 mm long and 60 mm high, thus rather elongated and slender. It is remarkably narrow (if not due to post-mortem compression), by comparison with most other 'osteolepiforms', and its overall aspect can be described as a flattened, slightly curved plate (Text-figs 10, 11B). The anterior end of the dentary is blunt (De, Text-fig. 10), the anteroventral lamina of the infradentary 1 is very deep and its anterior end is imbayed by a notch (n.Inf, Text-fig. 10).

The suture between the dentary and infradentaries (sut, Text-fig. 10) is not visible anteriorly and no suture between the individual infradentaries could be observed, although these are presumably present and masked by the external ornamentation, which consists of a fine ridge network. The overall shape, size and ornamentation of the mandible are

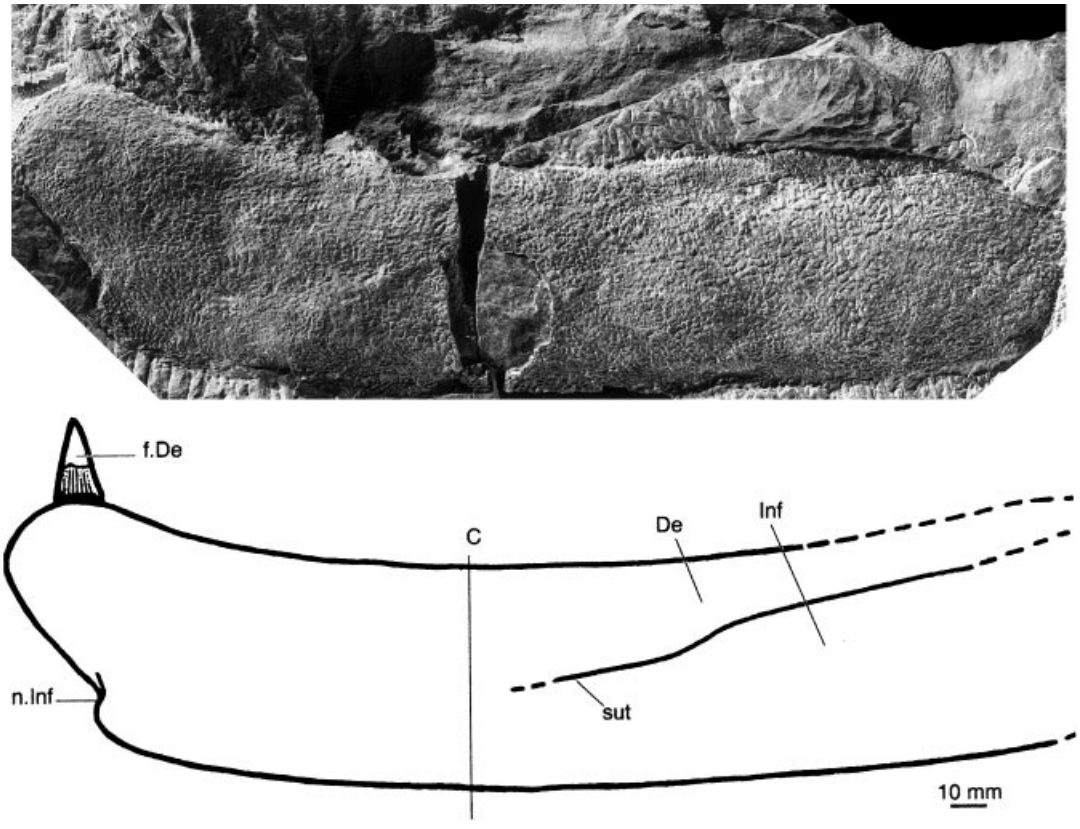


TEXT-FIG. 9. A–B, Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium. A, MNHN ARD 249, associated dorsal part of the right squamosal and preopercular, part of the right opercular, and extrascapular. B, MNHN ARD 250, posteroventral part of the left cheek.

very similar to those of the mandible referred to *Platycephalichthys skuenicus* by Vorobyeva (1962, pl. 17, fig. 2) but its internal side is more similar to that of *Platycephalichthys bischoffi* (Vorobyeva 1962, pl. 16, fig. 1B), in its elongated and slender adductor fossa (add.foss, Text-fig. 11A) and very slender posterior coronoids.

The anterior end of the dentary bears a fang pair (f.De, Text-fig. 10), as in *Cabonnichthys, Eusthenodon, Hyneria, Mandageria*, and *Platycephalichthys*, and contrary to *Eusthenopteron* and *Jarvikina*. The dentary and coronoid fangs (Text-fig. 12A) are conical in shape, yet slightly compressed laterally, and show strong longitudinal ridges, except near their apex.

A horizontal section through the middle part of the first coronoid fang (Text-fig. 12B) shows an eusthenodont structure (Schultze, 1969, 1970). The orthodentine is simply and irregularly folded, with first and second degree branchings. The bone of attachment only extends over a short distance between the folds and there seem to be traces of osteodentine trabeculae inside the pulp cavity. It should be noted that, if the pulp cavity is filled with osteodentine, the tooth histology would be similar to that of *Platycephalichthys bischoffi* (Vorobyeva 1977, fig. 21B).



TEXT-FIG. 10. Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 251, left mandible in lateral view. Transverse section C is reconstructed in Text-figure 11B.

The prearticular (prart, Text-fig. 11A–B) is smooth, except along its dorsal edge where tiny, rounded denticles are present (de.prart, Text-fig. 11A).

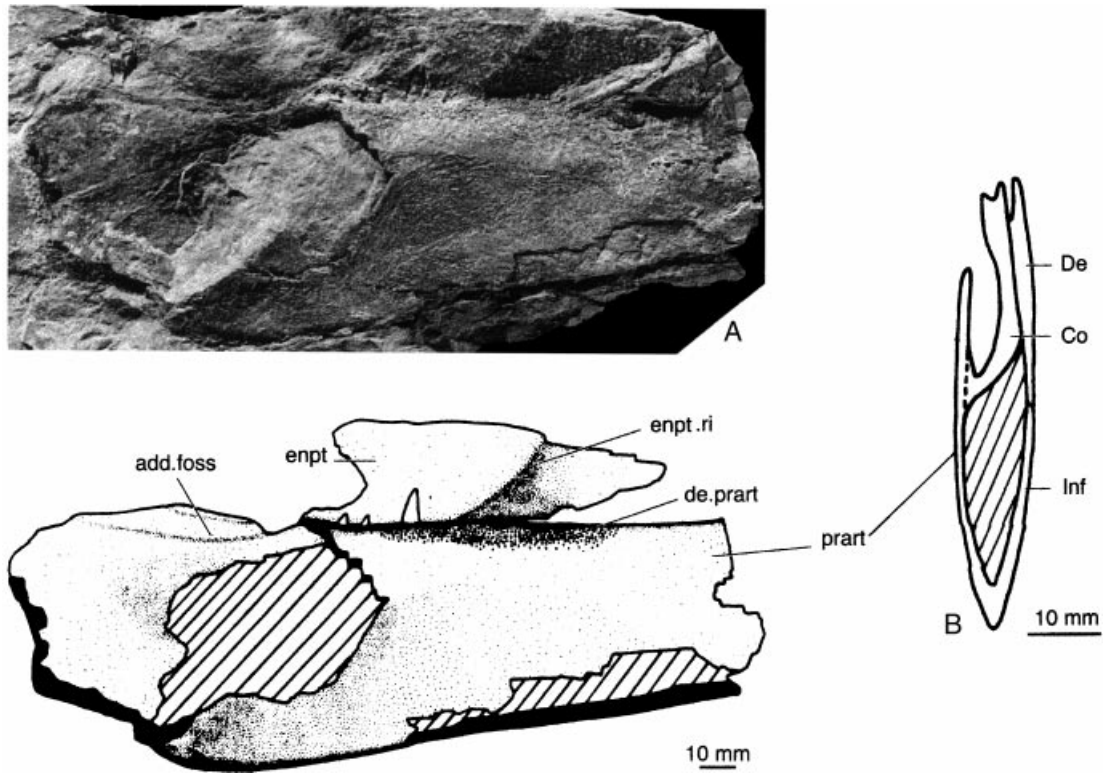
According to Thomson (1967, fig. 10), there is a more or less constant proportional relationship among osteolepiforms between the length of the lower jaw and the length of the post-parietal and parietal shields. An estimation of the cranial proportions for this material results in a skull-roof length (extrascapular excluded) of approximately 300 mm. This accords with that of the largest individuals of *Eusthenodon wängsjöi* (e.g. MGUH VP P1477) described by Jarvik (1952, pl. 18), who estimated the total length of this fish to have been approximately 2·25–2·5 m (considering that the body length of the 'osteolepiforms' is generally about 4·5–5 times that of the skull). This estimated size also agrees with the total length of *Hyneria* (Thomson 1968) and the two *Platycephalichthys* species (Vorobyeva 1959).

Postcranial skeleton (Text-fig. 13A–B). The shape of the ventral part of the clavicle, the only known element of the dermal shoulder girdle, is of generalized tristichopterid type, and its ornamentation consists of large, roughly parallel and interconnected ridges.

The only available part of the squamation consists of isolated scales (Text-fig. 13A–B) and a disorderly dermal fin ray assemblage. The scales are *Eusthenopteron*-like; that is, rounded, very thin and with a median drop-shaped knob on their internal surface.

DISCUSSION

The two specimens described here almost certainly belong to the Tristichopteridae. In the smaller one, the bone pattern of the skull roof, the shape of the subopercular and infradentaries, the bone and scale

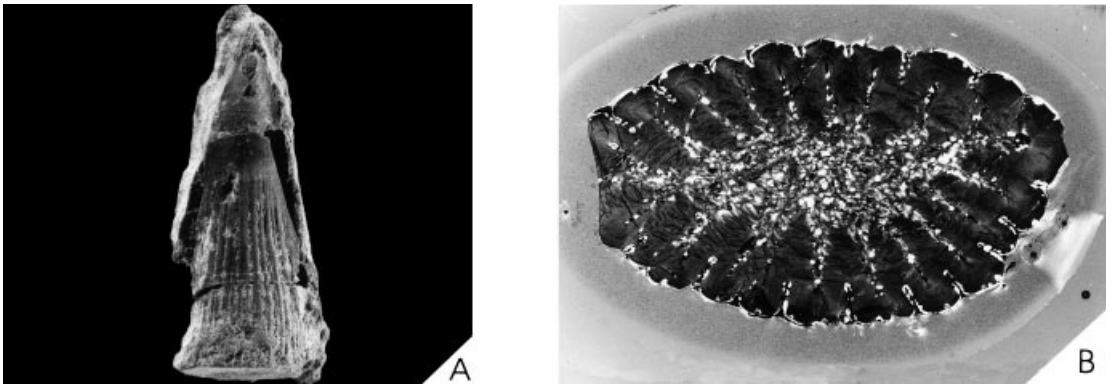


TEXT-FIG. 11. A–B, Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium. A, MNHN ARD 251, left mandible in medial view with associated entopterygoid. B, transverse section, reconstructed from the break in the midpart of the specimen at the level indicated C in Text-figure 10.

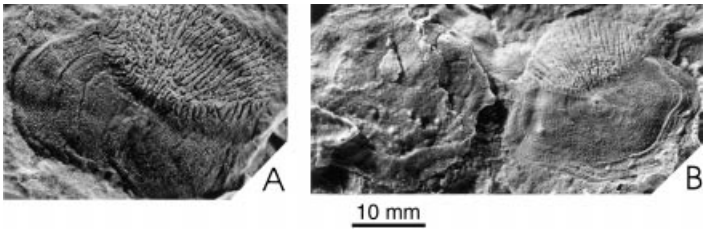
ornamentation, and the size of the fish are practically identical to those of *Eusthenodon* and fall within the range of variation of the type species of this genus *E. wängsjöi*.

The determination of the larger specimen is more difficult. However, it displays an assemblage of features which support tristichopterid affinities. The distribution of these characters is as follows: (1) The presence of a postspiracular, though only inferred here from indirect evidence, is characteristic of the Tristichopteridae. (2) The cheek shows a general 'osteolepiform' pattern, with a large squamosal which separates the rather narrow preopercular from the maxilla. (3) The snout shows a tristichopterid pattern. (4) The shape, size and ornamentation of the lower jaw is quite similar to that of the tristichopterid *Platycephalichthys.* (5) The tooth histology is of eusthenodont type (i.e. found in *Eusthenodon*, *Platycephalichthys* and *Litoptychius*), but is also quite similar to that of *Panderichthys*. (6) The anterolateral margin of the supratemporal shows no lateral expansion, as in the tristichopterid *Hyneria lindae* (Thomson 1968), *Mandageria fairfaxi* (Johanson and Ahlberg 1997) and *Platycephalichthys skuenicus* (Vorobyeva 1977, pl. 14). In addition, it shows a short anterolateral margin toward the anterior margin of the spiracular fenestra.

According to Ahlberg and Johanson (1998), the loss of cosmine and extratemporal bones, the narrowing of the otic part of the skull and lengthening of the snout, orbitotemporal region and corresponding parts of the lower jaw are derived characters which occurred within the 'osteolepiform' grade of the Tetrapodomorpha. Futhermore, the rhizodontids, derived tristichopterids and the clade including panderichthyds and tetrapods show a remarkable parallelism in their dramatic increase in size, reduction or loss of their median fins, gain of diphycercal tails with a low aspect ratio, and development of a pair of fangs at the



TEXT-FIG. 12. A–B, Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium. A, MNHN ARD 257, coronoid fang; ×2. B, coronoid fang histology, ×10.



TEXT-FIG. 13. A–B, Tristichopteridae gen. et sp. indet., Late Famennian, Langlier quarry, Durnal, Belgium. A, MNHN ARD 254, scale in external view. B, MNHN ARD 255, scales in internal and external views.

lower jaw symphysis. The characters that can be observed on this large form from Belgium are the very large size of the fish, a lengthening of the orbitotemporal region and corresponding parts of the lower jaw, and a pair of fangs at the lower jaw symphysis.

Most of the features of these large fish are characteristic of the derived Tristichopteridae, and this is probably where it belongs. However, according to Johanson and Ahlberg (1997, pp. 42–43) 'Tristichopterids are characterised by the presence of a postspiracular bone, a three-lobed caudal fin, the anteroposterior orientation of the crista parotica, absence of an extratemporal, and round, non-cosmoid scales with a median ridge on the inner surface (Jarvik 1980; Long 1985; Young *et al.* 1992; Cloutier and Ahlberg 1996). Only the first two of these characters are likely to be synapomorphies, the third is of uncertain distribution, whereas the fourth and fifth are more widely distributed among the Osteolepiformes'. This restrictive definition leaves few characters that can actually be observed on this material.

The size of the fish, along with the inferred presence of a postspiracular, the pattern of the cheek and snout bones, the overlap of the maxilla by the squamosal, the scale and bone ornamentations, and the tooth histology are suggestive of either *Eusthenodon* or *Platycephalichthys*. It could, therefore, be a *Eusthenodon* species with unusual mandible and supratemporal shapes, or a *Platycephalichthys* species with an unusual snout pattern. It is also important to note that the lower jaw of *P. bischoffi* has not been found in connection with the skull designated as the holotype of *Platycephalichthys bischoffi* (Vorobyeva 1959). However, the holotype of *P. skuenicus* is the mandible, which is strikingly similar to that in the material from Belgium (Vorobyeva 1962, pl. 7, fig. 2). It is important to note that the *Eusthenodon* material is almost complete and the classic Greenland material clearly represents a single species. *Platycephalichthys* is less well understood, and it is not entirely certain that the different species assigned to it really form a natural group.

The presumed tristichopterid *Hyneria lindae*, from the Upper Devonian of Pennsylvania, described by Thomson (1968), is also problematical. Thomson erected the new genus *Hyneria*, on the sole basis of the ornamentation of the dermal bones of the skull and the shoulder girdle, which he described as follows: 'On the skull elements, the dentine ridges form an extremely regular pattern of small symmetrical spaces enclosed by tuberculated ridges. On the shoulder girdle, the ridges tend to be more parallel and the enclosed lacunae are therefore elongated (in the direction of the axis of the cleithrum)' (Thomson, 1968, p. 3). The ornamentation of the large specimen from Belgium matches exactly this definition.

Hyneria and *Platycephalichthys* are unfortunately incompletely described or known, although Ahlberg and Johanson (1997, p. 671) assumed that '*Hyneria* (admittedly on very slender evidence) seems to be at least as derived as *Platycephalichthys*', which is of little help in determining this Belgian tristichopterid.

Ahlberg and Johanson (1997) have suggested a Laurussian origin for the Tristichopteridae. All the most primitive tristichopterids (*Eusthenopteron, Jarvikina, Platycephalichthys, Spodichthys, Tristichopterus*) have been found in Laurussia (i.e. Laurentia + Baltica). The most advanced tristichopterids (*Cabonnichthys, Mandageria*) come from Gondwana. The only tristichopterid found in both Devonian continents is *Eusthenodon* (Laurussia: Greenland, Russia and now Belgium; Gondwana: South Africa and Australia). Nevertheless, Ahlberg and Johanson (1997, p. 671) pointed that 'although *Mandageria* and *Cabonnichthys* are closely related, the sister group of *Mandageria* is the Laurussian genus *Eusthenodon*. This seems to imply that the Gondwanan tristichopterids were part of a widely distributed and freely dispersing fauna rather than a geographically isolated radiation'.

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APPENDIX

Abbreviations

In text-figures: add.foss, adductor fossa; ar.pal, area for palatoquadrate dorsal process (paratemporal process); Co, coronoid; De, dentary; de.prart, prearticular denticles; der.f, pair of dermopalatine fangs; enpt, entopterygoid; enpt.ri, entopterygoid ridge; Ext, extrascapular; f.De, dentary fang; fe.exch.n, fenestra exchoanalis notch; fe.sc, fenestra in ventral wall of infraorbital sensory canal dorsally to spiracular canal; gr, groove for ridge-like part of otico-occipital bounding fossa bridgei laterally; gr.Su, supratemporal groove; gr.sub, groove for submandibular bones; i.hyd, notch dorsally to dorsal articular area for hyomandibular; i.spir, spiracular notch; Inf 3, posterior part of the infradentary 3; Inf 4, infradentary 4; Inf, infradentaries; It, intertemporal; Ju, jugal; La, lacrimal; la.spir, ventral lamina of postparietal shield medially to dorsal part of spiracular tube; Ma, maxilla; Mpr, median postrostral; Mpra, anterior median postrostral; Mprp, posterior median postrostral; m.ri, median ridge; m.Su, short and straight antero-lateral margin of supratemporal; n.Inf, notch of the infradentary 1; Na, nasal; od.It, area of supratemporal overlapped by dorsal medial lamina of intertemporal; od.Ju, area of squamosal overlapped by jugal; od.La, area overlapped by lacrimal; od.Lj, area overlapped by lower jaw; od.Ma, area overlapped by maxilla; od.Op, area overlapped by opercular; od.Po, area overlapped by postorbital; od.Pop, area overlapped by preopercular; od.Pos, area overlapped by postspiracular; od.So, area overlapped by supraorbital; od.Sq, area overlapped by squamosal; od.Sup, area overlapped by posterior supraorbital; om, orbit margin; Op, opercular; Pa, parietal; pin.pl, pineal plate; pl.Inf 4, infradentary 4 pit-line; pl.Pa, parietal pit-line; pl.Sq, squamosal pit-line; pm.Pa, posterior margin of parietal; Pmx, premaxilla; Pop, preopercular; Ppa, postparietal; prart, prearticular; Qj, quadratojugal; r.a, rough area; ri.ioc, ridge housing infraorbital sensory canal; s.dep, small depression situated at the anterior dorsal end of supratemporal; Sq, squamosal; Su, supratemporal; sut, suture; Ta, tabular; Te, tectal.

Institutions: MNHN, Muséum National d'Histoire Naturelle de Paris, France; MGUH VP, Geological Museum of the University of Copenhagen.