A NEW TRISTICHOPTERID (SARCOPTERYGII, TETRAPODOMORPHA) FROM THE UPPER FAMENNIAN EVIEUX FORMATION (UPPER DEVONIAN) OF BELGIUM

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Abstract: Additional material of a large specimen of tristichopterid fish from the Upper Famennian Evieux Formation of Belgium is described. This large fish was previously assigned to Tristichopteridae gen. et sp. indet. due to the lack of diagnostic anatomical data. New available material consists of the internal surface of the parietal shield, vomers and anterior part of the parasphenoid, subopercular and submandibulo-branchiostegal bones, and an internal view of the anterior part of the mandible. A possible autapomorphy of the new form from Belgium, *Langlieria socqueti* gen. nov. et sp. nov., is the absence of marginal teeth on the vomer except on its most lateral part. Apart from these features, it only differs from the genus *Mandageria* from Australia in the

absence of marginal teeth between the dentary fang and the mandibular symphysis, in the presence of a raised marginal crest lateral to the anterior coronoid fang, and in the presence of numerous small marginal teeth on the premaxilla. It differs from the cosmopolitan genus *Eusthenodon* in a number of respects: the supratemporal, tabular, and postparietal bones are superficially fused, as are the intertemporal and parietal bones, the dermal ornament is proportionally very fine, and the denticulated field of the parasphenoid stands proud rather than being recessed into the body of the bone.

Key words: Belgium, biogeography, Late Devonian, phylogeny, Tetrapodomorpha, Tristichopteridae.

THE discovery of large tristichopterids in the Upper Devonian of Belgium (Clément 2002) marked the beginning of a revision of the Devonian vertebrate palaeontology collections of the main institutions of Belgium (Liège University, Royal Institute of Natural Sciences, Brussels, and Catholic University of Louvain-la-Neuve).

Almost all the historical material of Famennian vertebrates from Belgium was collected during the late nineteenth century. Few specimens were described and figured at this time (Lohest 1888*a*, *b*) with some more descriptions 50 years later (Leriche 1931). More recently, some coccosteid (Placodermi, Arthrodira) remains have been described from the Famennian of Esneux (Lelièvre 1982), as well as a new actinopterygian genus from the Early Famennian of La Fagne (Taverne 1997). The Palaeozoic vertebrate faunas of northern France and Belgium were reviewed some 10 years ago (Blieck and Lelièvre 1995; Cloutier and Candilier 1995; Derycke *et al.* 1995).

Recent fieldwork has been undertaken in various Middle and Upper Famennian localities of Belgium. The Famennian outcrops of Belgium are located beneath Namur and Liège in the so-called Dinant Synclinorium. Most of the quarries, used since the 19th century for making building stones, are now abandoned but still accessible and a few of them are still intensively exploited. Prospecting in these old and current quarries has resulted in the findings of important new material.

New occurrences, found both in collections and in the field, have already been recorded. These include a new groenlandaspidid placoderm (Janvier and Clément 2005), a rhynchodipterid lungfish (Clément and Boisvert 2006) and an *Ichthyostega*-like tetrapod (Clément *et al.* 2004). Some other sarcopterygians are still under study (dipnoans, possible megalichthyids, rhizodontids, osteolepidids) and will be described in separate papers.

The diversity and abundance of vertebrate fossil remains (mostly placoderms and sarcopterygians) already

met with in a short time during field trips, as well as material housed in the Belgian museums, show that the Famennian vertebrate localities of Belgium are among the best sites in the world for palaeoenvironmental and biostratigraphical studies of Upper Devonian marginal marine and freshwater environments.

The material described herein comes from the counterpart of a large isolated dolomitic sandstone block that provided remains of two tristichopterid fishes (Clément 2002). The large dolomitic sandstone block bearing numerous small scales and large dermal bones was collected in 1995 during the IGCP 328/SDS Joint Field Trip Boulonnais (France) – Ardenne (Belgium) (Blieck 1995). This block was found among other isolated blocks, recently detached from the approximately 30 meter-high cliff of the Langlier quarry. This locality is located between the towns of Dorinne and Durnal, Namur Province, Belgium (Text-fig. 1). This block is housed in the Palaeontology Department, Muséum national d'Histoire naturelle, Paris, France (MNHN). The fossil material present on this block consisted of two large tristichopterid fishes. One of them was referred to the taxon *Eusthenodon wangsjoi* Jarvik and the other, much larger, was determined as Tristichopteridae gen. et sp. indet. (Clément 2002). The lack of anatomical data, especially of diagnostic features precluded a more precise identification.

Recently one of us (G. C.) visited the Palaeontology Collection of Liège University, Belgium. A thick block of dolomitic sandstone turned out to be the counterpart of the block housed at the MNHN. This counterpart is now also housed in the Palaeontology Department, Muséum national d'Histoire naturelle, Paris, France (MNHN). This counterpart presents some important new anatomical data (Text-fig. 2) allowing us to describe this large tristichopterid fish as a new genus and species.
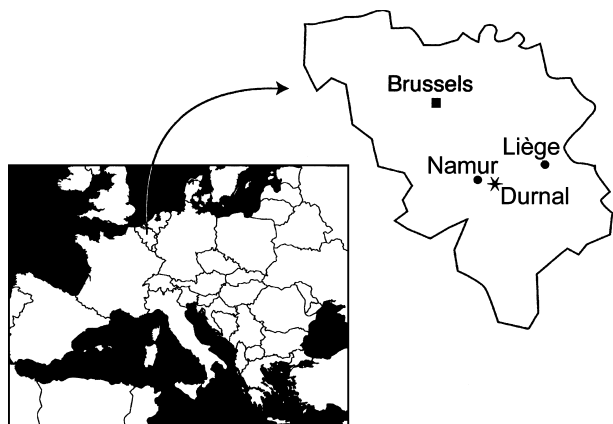
TEXT-FIG. 1. Locality map of the Langlier quarry, near Durnal, Namur Province, Belgium.

MATERIAL AND METHODS

Dermal elements present on the counterpart have been removed with hydrochloric acid in order to obtain a natural mould from which an elastomer cast could be made. The anterior part of the skull roof and palate has been acid prepared in two steps: a preliminary preparation (Text-fig. 3) and a further preparation revealing more anatomical data on the parasphenoid, vomers and premaxillae (Text-fig. 4).

This method provided a positive cast of the internal side of the skull roof and snout, part of the palate, left subopercular, left submandibulo-branchiostegal, and the anterior part of the left gular. Fine details such as small ridges of ornamentation, sutures of the skull, and tiny teeth are clearly visible on the cast.

The anterior region of the left mandible present on the large block collected in 1995, the lateral side of which having been previously mechanically prepared (Clément 2002, fig. 10), has also been treated by removing the bone with hydrochloric acid in order to make an elastomer cast of its lingual side. Furthermore, an isolated right dermopalatine was found by one of us (G. C.) in 2003 in a dolomitic nodule. It also comes from the Langlier quarry but from a layer situated on the cliff opposite to the tristichopterid-bearing layer. This specimen has been prepared mechanically.

## GEOGRAPHICAL AND GEOLOGICAL SETTING

The Langlier quarry is situated in the northern 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 estuary or tidal delta influences.

The fossil-bearing horizon is most probably situated in a fossil channel visible in the middle of the cliff, up to the area where the isolated blocks were found (J. Thorez, pers. comm. 2004). It is unfortunately impossible to access the fossil layer without professional climbing equipment.

Institutional abbreviations. MNHN, Muséum National d'Histoire Naturelle, Paris, France.

Anatomical abbreviations. ant.pr, anterior process of the dermopalatine; ar.pal, area for the palatoquadrate dorsal process (paratemporal process); aSo, anterior supraorbital bone;

TEXT-FIG. 2. *Langlieria socqueti* gen. nov. et sp. nov., Upper Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 259; anterior part of the skull roof in ventral view (half right), with left subopercular (MNHN ARD 260, bottom left), right submandibulo-branchiostegal plate (MNHN ARD 261, middle left), and anterior part of the left gular (MNHN ARD 262, top left) in external views. Scale bar represents 5 cm.
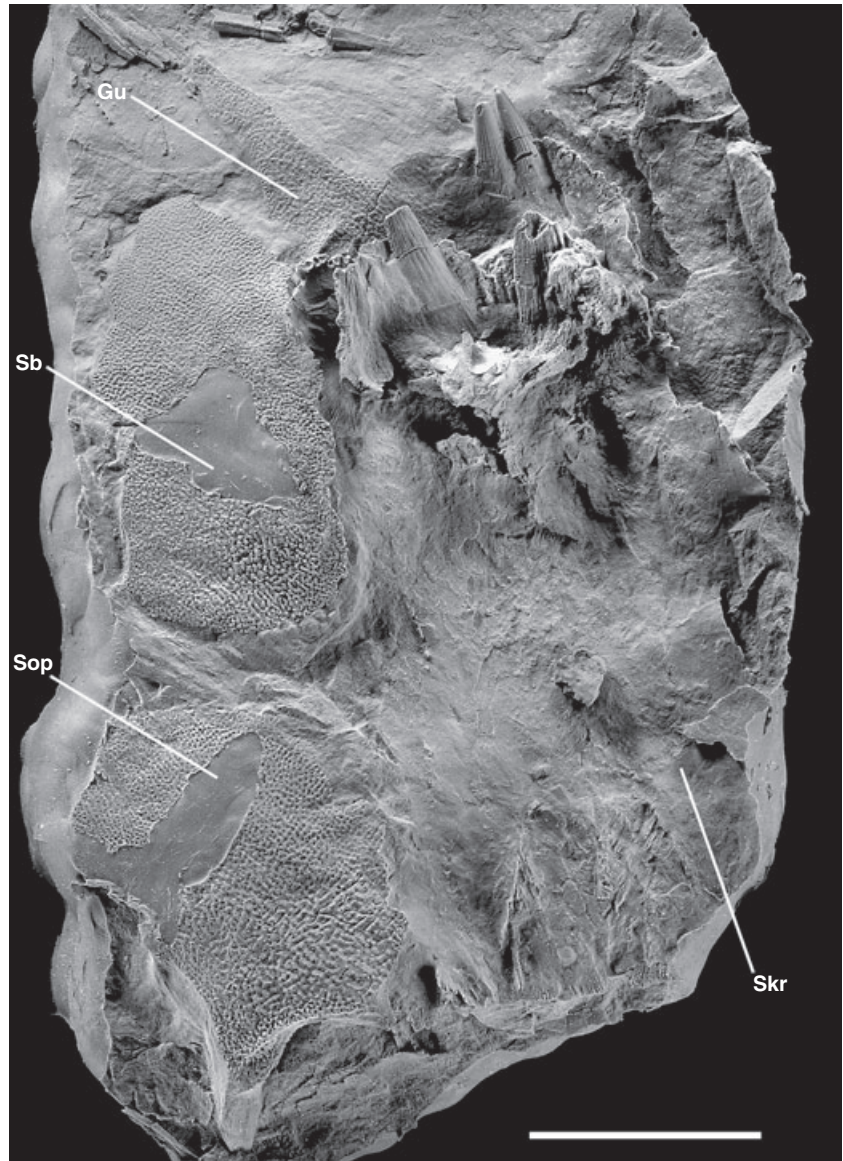
b.Psp, broken area of the parasphenoid; ch, choana; co.Vo, postero-lateral corner of the vomer; d.Co1, small marginal teeth on the anterior coronoid; d.Psp, denticulated area of the parasphenoid; Der, dermopalatine bone; Ect, ectopterygoid bone; f.Co1, anterior coronoid fang; f.De, dentary fang; f.Der, dermopalatine fang; f.Pmx, premaxillary fang; f.Vo, vomerine fang; fl.Sp, splenial flange; Gu, gular plate; la.spir, ventral lamina of the postparietal shield medially to the dorsal part of the spiracular tube; Int, intertemporal bone; m.t, marginal dentition of the dermopalatine; mPro, median post rostral bone; n.spir, spiracular notch; o.m, orbital margin; od.Ext, area overlapped by the lateral extrascapular; od.La, area overlapped by the lachrymal; od.Lro, area overlapped by the lateral rostral bone; od.Man, area overlapped by the mandible; od.Op, area overlapped by the opercular bone; od.Po, area overlapped by the postorbital bone; od.Pop, area overlapped by the preopercular bone; od.Ppa, area overlapped by the postparietal; od.Ps, area overlapped by the parasymphysial dental plate; od.pSo, overlapped area for the posterior supra-orbital bone; od.Qj, area overlapped by the quadratojugal; od.Sop, area overlapped by the subopercular bone; od.Su, area overlapped by the supratemporal; or.Pmx, ornamented surface of the premaxilla; or.Ppa, ornamented surface of the postparietal; Pa, parietal bone; pi, pineal area; pp.Vo, posterior process of the vomer; Ppa, postparietal bone; Pre, prearticular bone; Psp, parasphenoid; rp.f, replacement pit for the dermopalatine fang; Sb, submandibulo-branchiostegal plate; sf.Vo, small vomerine fangs; Skr, anterior part of the skull roof with vomers and anterior part of the parasphenoid; Sop, subopercular bone; Su, supratemporal bone; sym, symphysial region of the mandible; Ta, tabular bone; t.De, marginal dentition of the dentary; t.Pmx, marginal dentition of the premaxilla; Te, tectal bone; vl.Vo, vertical lamina of the vomer; Vo, vomer.
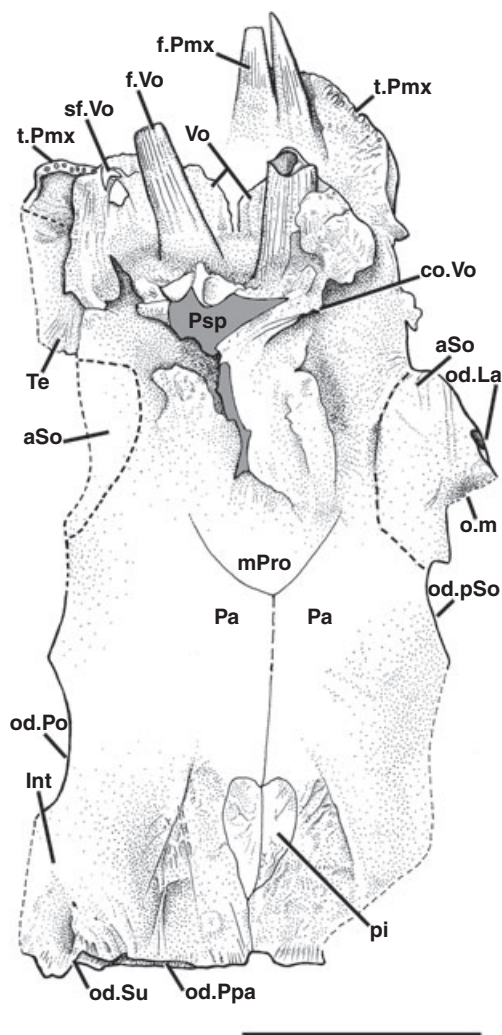
TEXT-FIG. 3. *Langlieria socqueti* gen. nov. et sp. nov., Upper Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 259; holotype; anterior part of the skull roof in ventral view with vomers and anterior part of the parasphenoid. Same specimen as in Text-figure 4 before further acid preparation. Grey area shows the broken part of the parasphenoid. Scale bar represents 5 cm.

SYSTEMATIC PALAEONTOLOGY

SARCOPTERYGII Romer, 1955
OSTEOLEPIFORMES Berg, 1937
TRISTICHOPTERIDAE Cope, 1889

Genus LANGLIERIA gen. nov.

Derivation of name. From Langlier quarry, source of the material.

Type and only known species. *Langlieria socqueti* sp. nov.

Diagnosis. As for the single known species, *Langlieria socqueti* gen. nov. et sp. nov., below.

Langlieria socqueti gen. nov. et sp. nov.,
Text-figures 2–4, 6–7

2002 Tristichopteridae gen. et sp. indet., Clément 577, 582–591, fig. 5–13.

Derivation of name. Specific name in honor of the Socquet family and relations in recognition of their important contributions to research in the Upper Devonian of Belgium.

Holotype. MNHN ARD 259, (Text-figs 2–4), anterior part of the skull roof in ventral view with vomers and anterior part of the parasphenoid, preserved in part and counterpart.

Locality. Langlier quarry, Namur province, Belgium.

Horizon and age. Evieux Formation, Upper Famennian, Upper Devonian.

Diagnosis. Large tristichopterid characterised by the following combination of features, some of which are primitive for the Tristichopteridae, some characteristic for a derived clade within the group, and some of uncertain phylogenetic significance.

Primitive. Denticulated field on parasphenoid stands proud of the body of the bone, forming a distinct 'prow' anteriorly, rather than being recessed into the body of the bone; raised marginal crest present on anterior coronoid; round, thin, moderately large scales.

Derived. Dentary fang pair present; anteriormost tooth of premaxillary tooth row enlarged into 'pseudofang'; all fangs and pseudofangs equipped with nonserrated cutting edges; marginal teeth absent on vomers; pineal series large, kite-shaped and located between posterior halves of parietals.

Uncertain phylogenetic significance. Proportionately fine ornament; superficial fusion of supratemporal, tabular and postparietal bones and of intertemporal and parietal bones; marginal premaxillary teeth small and numerous (at least 29 but probably more); postparietal shield proportionately short, and broad posteriorly.

Remarks. Although *Langlieria socqueti* presents a unique character combination, its only apparent autapomorphy is the absence of a vomeral tooth row. The fine ornament and the skull fusion are shared with *Mandageria* (Johanson and Ahlberg 1997), and small numerous premaxillary teeth with *Jarvikina* (Vorobyeva 1962, 1977), though the latter genus lacks enlarged pseudofangs,

TEXT-FIG. 4. *Langlieria socqueti* gen. et sp. nov., Upper Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 259; close-up on the anterior part of the palate with vomers and anterior part of the parasphenoid in ventral view. Same specimen as in Text-figure 3 after further preparation, i.e. removing all the bone with hydrochloric acid in order to make a new and more complete elastomer cast. White arrows show the small vomerine fangs. Scale bar represents 10 mm.
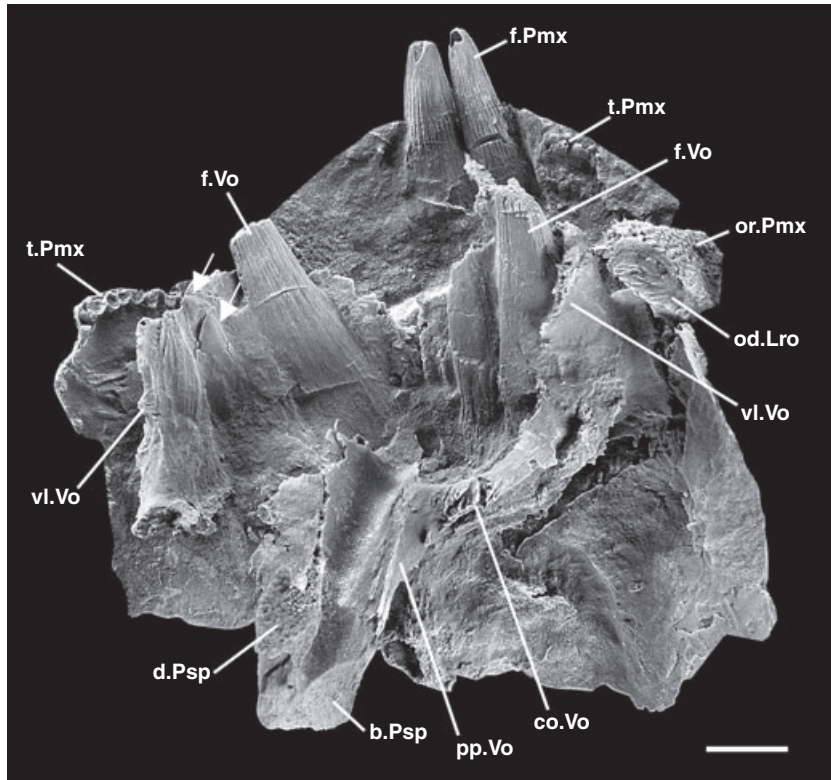
while the proportions of the postparietal shield resemble *Platycephalichthys skuenicus* (Vorobyeva, 1977). We place it in a new binomen principally because it does not obviously form a clade with any known tristichopterid genus. *Langlieria* is distinct from *Mandageria* in two regards: *Langlieria* lacks marginal teeth on the dentary between the dentary fang and the mandibular symphysis, and has a vertical lamina on the anterior coronoid lateral to the anterior coronoid fang.

Description

Skull roof. The near-complete parietal shield is visible in internal view (Text-figs 2–3). It is proportionally long and slender, as in *Mandageria* (Johanson and Ahlberg 1997) and *Eusthenodon* (Jarvik, 1952) and does not seem as wide as in *Cabonnichthys* (Ahlberg and Johanson 1997) or *Platycephalichthys* (Vorobyeva 1959, 1962, 1977), particularly in the snout region. The median suture separating the parietal bones is straight and only interrupted by the pineal bones. The median suture of the parietals is usually interdigitate in *Eusthenodon wangsjoi* from the Famennian of East Greenland but this feature is variable within this species (Jarvik 1952, 1985). It is straight in *Mandageria* and *Cabonnichthys*, two derived tristichopterids from the Famennian of Australia (Johanson and Ahlberg 1997; Ahlberg and Johanson 1997). The kite-shaped series of pineal bones (Text-figs 2–3) is close to the posterior margin of the parietal shield but does not reach it. The position of the pineal area in relation to the posterior margin of the parietals is known to be highly variable in *Eusthenodon* (Jarvik 1985). However, a kite-shaped pineal area in

a posterior position seems to be present in all derived tristichopterids since it is also known in *Mandageria* (Johanson and Ahlberg 1997, fig. 10) and *Cabonnichthys* (Ahlberg and Johanson 1997, fig. 4). The pineal area is rounded or oval in shape and in a more anterior position in *Eusthenopteron* (Jarvik 1980, fig. 116) and *Jarvikina* (Vorobyeva 1977, fig. 42).

The intertemporal-parietal suture is not discernible. The posterior part of the intertemporal is however distinguishable from the posterior part of the parietal due to the excellent preservation of the intertemporal-supratemporal articular complex. This complex extends slightly posterior to the posterior margin of the parietals.

A large and regular embayment is present on the lateral margin of the parietal although the intertemporal also most probably contributes to the posterior region of this embayment. Into this large rounded notch probably fitted the postorbital bone (Text-figs 2–3).

A V-shaped faint suture probably delimitates the posterior part of the median postrostral (Text-figs 2–3). The posterior tip of this suture is situated at the centre of the anterior portion of the skull roof. This is similar to the condition in *Mandageria* (Johanson and Ahlberg 1997, fig. 6) and *Eusthenodon* (Jarvik 1952, fig. 23) but different from *Cabonnichthys* (Ahlberg and Johanson 1997, fig. 5) and *Eusthenopteron* (Jarvik 1980, fig. 121) where the parietal-median postrostral suture is more anteriorly located. However, this feature seems to be highly variable since some *Eusthenodon* specimens (number P. 1478, Jarvik 1952, pl. 13 and number P. 1473, Jarvik 1952, pl. 15) show the *Eusthenopteron* condition. No suture is visible in the snout region due to the preservation and presence of palatal elements. The external bone pattern of the snout has been figured in Clément (2002, fig. 7).

Both anterior supraorbital bones, firmly attached to the skull roof, are discernable although their sutures are very faint (Text-figs 2–3); the lateral margin of the left bone, which is better preserved, shows an overlap area for the lachrymal. In internal view the posterior part of the bone is smooth and strongly concave suggesting the proximity of the orbit. Unfortunately the orbital margin itself is not visible, but it is evident that the orbit was situated at a level somewhat posterior to the anterior margin of the parietals. Disregarding the intraspecific variation in the skull roof bone pattern, it seems that *Eusthenopteron* and *Cabonnichthys* present an orbit situated behind the level of the suture between the median postrostral and parietals, whereas it is situated in front of this suture in *Mandageria*. As an example of intraspecific variation, *Eusthenodon wangsjoi* can present the orbit behind (Jarvik 1952, pl. 13), at the same level (Jarvik 1952, pl. 14) or in front (Jarvik 1952, pl. 20) of the median postrostral-parietal suture.

Premaxilla. Two enlarged teeth are present at the midline of the snout (Text-figs 2–4). These teeth are antero-posteriorly flattened with pronounced cutting edges. They are about half the size of the vomerine fangs. Despite the distortion of the specimen, it seems that the enlarged premaxillary teeth lie in line with the premaxillary tooth row (as in *Eusthenodon* and *Mandageria*, two other tristichopterids with enlarged premaxillary teeth). They do not seem to be located posterior to the premaxillary tooth row on a posterior premaxillary process, as in the megalichthyids *Megalichthys* (Jarvik 1966) and *Ectosteorhachis* (Thomson 1964). As these enlarged teeth lie within the tooth row and do not occur in pairs (i.e. two standing fangs, or a fang + replacement pit, as seen for example on the vomers or anterior end of the dentary) we designate them as 'pseudofangs' rather than true fangs. Similar enlarged premaxillary teeth are seen in *Mandageria* (Johanson and Ahlberg 1997), *Cabonnichthys* (Ahlberg and Johanson 1997), *Eusthenodon* and *Hyneria* (pers. obs.) but not in more primitive tristichopterids such as *Eusthenopteron* (e.g. Jarvik 1980). The premaxillary tooth row is composed of numerous very small pointed teeth (at least 29 but probably more). The number of teeth is greater than in the derived tristichopterids *Mandageria* (Johanson and Ahlberg 1997, fig. 11) and *Cabonnichthys* (Ahlberg and Johanson 1997, fig. 8) and much greater than in the primitive tristichopterid *Eusthenopteron* (Jarvik 1980). The posterior part of the premaxilla is fractured but otherwise well preserved on the left side. It has a tapered end and the overlap area for the lateral rostral is well-developed dorsally (Text-fig. 4). The ornamentation of the posterior part of the premaxilla is composed of thin and numerous anastomosed ridges, similar to the rest of the ornamentation of the head in this respect (Clément 2002).

Vomers, dermopalatine, and parasphenoid. The vomers meet in the midline in front of the parasphenoid (Text-figs 2–4). The posterior process of the vomer runs along the lateral margin of the parasphenoid and seems to be strongly attached to it (clearly visible on the Text-fig. 4, same specimen as in Text-fig. 2 after further preparation).

The vomers present the usual fang pairs. These fangs are oval in section and present cutting edges, but these edges are less pronounced that those of the enlarged teeth of the premaxilla.

Two fangs are present on the left vomer whereas only one is present on the right one. There are two small free-floating fang tips present antero-ventral to the replacement pit (Text-figs 3–4). These are located along the internal wall of the vertical lamina. They are triangular in shape and much flattened antero-posteriorly with prominent but nonserrated cutting edges. The smallest one is situated ventral to the other one. It appears that these are unfinished replacement teeth that were still growing on dental papillae at the time of death. The odontogenetic significance of two replacement teeth growing, at one time and on one row, in the same replacement pit, falls outside the scope of this paper. However, we note that a similar pair of vomerine replacement fangs can be seen in a CT-scanned specimen of *Eusthenopteron* (Ahlberg 2007, 'additional imagery').

An interesting feature is the absence of a tooth row on the blade-like vertical lamina of the vomer, with the possible exception of its most lateral part. All other tristichopterids have a tooth row although the condition is not clear in *Hyneria*, a large derived tristichopterid from the Famennian of Pennsylvania (Thomson 1968).

The vomers and the anterior part of the parasphenoid together form a solid complex, which is strongly connected to the internal surface of the skull roof. In this specimen, the parasphenoid has been broken anteriorly but the anterior end of the parasphenoid, although slightly displaced, is still articulated with the vomers and firmly attached to the skull roof. This condition is also known in distorted specimens of *Platycephalichthys* (Vorobyeva 1962, pl. 9, figs 2, 11), and *Jarvikina* (Vorobyeva 1962, pl. 3 ['*Eusthenodon*' wenjukowi] and 1977, pl. 11, figs 6–7).

The lateral edge of the posterior process of the vomer is not straight or slightly concave (as seen on palatal reconstructions of other tristichopterids) but presents a strong corner with ridges on its margin revealing a strong attachment with the anterior process of the dermopalatine. Such a corner of the posterior process of the vomer is also known in *Platycephalichthys* (Vorobyeva 1962, pl. 9, fig. 2) and *Hyneria* but is absent in *Eusthenopteron* (pers. obs.). It represents an articulation surface for the dermopalatine, but its function and distribution among Tristichopteridae needs further consideration.

An isolated sarcopterygian dermopalatine (MNHN ARD 263, Text-fig. 5), most probably belonging to a large tristichopterid, has been found in another part of the Langlier quarry. In outline it is very elongated and narrow anteriorly, but this shape appears to be an artefact caused by the erosion and loss of the anteromesial part of the horizontal lamina; the complete bone probably resembled the corresponding element of *Mandageria*. A pair of large fangs occupies the middle part of the bone. Posterior to this fang pair the vertical lamina of the bone carries a marginal tooth row, but marginal teeth are absent anterior to the fangs. This agrees with the condition in *Mandageria* (Johanson and Ahlberg 1997, figs 7, 9A–B; Johanson et al. 2003, fig. 10) and possibly *Hyneria* (pers. obs.). Complete marginal tooth rows are known in *Cabonnichthys* (Ahlberg and Johanson 1997, fig. 7C–D) and *Eusthenopteron* (Jarvik 1980). The condition is not known in *Platycephalichthys* or *Eusthenodon*. Anteriorly the bone carries a long process that formed the posteromesial margin of the choana. The anterior tip of this process contacted the postero-lateral corner of the vomer.

The anterior part of the parasphenoid (Text-figs 2–4) is of the 'typical' tristichopterid pattern seen for example in *Eusthenopteron*, *Cabonnichthys* and *Mandageria* (Jarvik 1980; Ahlberg and Johanson 1997; Johanson and Ahlberg 1997): a deep and sharp longitudinal crest on the midline of the ventral side supports a raised, flat denticulated area (Text-fig. 4). This contrasts with the condition in *Eusthenodon* and *Hyneria* (pers. obs.) where the faintly concave denticulated area is slightly recessed into the body of the parasphenoid. The 'typical' pattern is evidently primitive, as it compares closely with the condition in *Panderichthys* (pers. obs. PEA) and less crownward tetrapodomorphs such as *Medoevia* (Lebedev 1995), *Gogonasus* (Long *et al.* 1997) and *Kenichthys* (Zhu and Ahlberg 2004). A deep and narrow longitudinal groove is present on the dorsal side of the parasphenoid. The posterior end of the parasphenoid has been sharply broken, with a straight oblique break. There is no evidence of the presence or absence of the so-called 'accessory vomers', narrow denticulated bones situated between the parasphenoid and entopterygoids, so far only known in *Mandageria* and *Cabonnichthys* (Ahlberg and Johanson 1997; Johanson and Ahlberg 1997).

Subopercular. A left subopercular (MNHN ARD 260, Text-figs 2, 6B) is also present in the new material. It can be assigned with some confidence to *Langlieria* since the subopercular assigned to *Eusthenodon wangsjoi*, coming from the same layer, is much smaller with an ornamentation composed of large ridges (Clément 2002). It should be noted here that the *Eusthenodon* subopercular, previously described as coming from the right side, is in fact a left subopercular (Clément 2002, fig. 3D).

The subopercular present in the new material has the characteristic shape for tristichopterids with a well-developed pointed anterior process separating the overlap area for the opercular from the preopercular [a similar anterior process, although less pronounced, is also known in *Gogonasus* (Long *et al.* 1997)]. A small antero-ventral process separates the latter from the overlap area for the postero-dorsal corner of the mandible. The dermal ornament consists of a network of fine anastomosed ridges, long and subparallel in the posterior region of the bone. It seems that most of the bones covering the posterior part of the head, e.g. the extrascapular and opercular (Clément 2002, figs 8–9), present these long and subparallel fine ridges, as does the submandibulo-branchiostegal bone (see below). The same condition is known in *Mandageria* (Johanson and Ahlberg 1997, fig. 2) and, to a lesser extent, *Cabonnichthys* (Ahlberg and Johanson 1997, fig. 4), but it does not seem to occur in other tristichopterids.
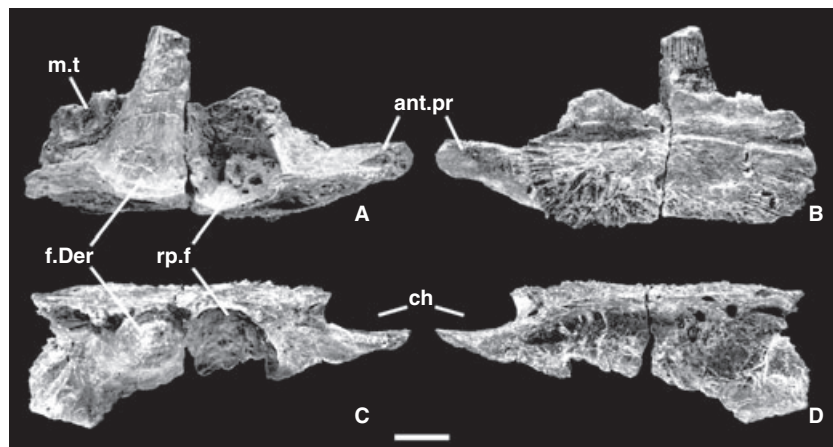
Submandibulo-branchiostegal. A long rectangular bone is identified as the right submandibulo-branchiostegal plate (MNHN ARD 261, Text-figs 2, 6A). Long and subparallel ornament ridges on one of the corners of the external surface identify this as the posterior region of the bone. The dorsal margin shows two overlap areas, one posterior for the subopercular and one anterior for the mandible. The posterior and ventral margins do not present any overlap area and the postero-medial corner is rounded as seen in the submandibulo-branchiostegal bone of *Eusthenopteron* (Jarvik 1944).

Gular. The anterior tip of the left gular (MNHN ARD 262, Text-fig. 2) is visible in front of the snout. It is acutely pointed, suggesting a slender shape for the anterior part of the head. The overlap area for a median gular is clearly visible.

Mandible. The external face of the anterior two thirds of the lower jaw, the internal face of the middle third of the jaw, and a cross-section at the level of the middle coronoid were described by Clément (2002). These demonstrated the presence of a large dentary fang pair, a feature common to all derived tristichopterids (as well as a number of other tetrapodomorph groups), and showed that the external face of the jaw is covered in fine ornament resembling that of *Mandageria* but quite unlike that of *Eusthenodon*. We are now able to supplement this account with a description of the internal face of the anterior part of the jaw, from the symphysis to the middle coronoid that reveals some phylogenetically informative characters (Text-fig. 7).

The marginal tooth row along the dentary consists of small and pointed teeth. There do not seem to be any small teeth of the dentary lateral to the fang pair and there are no teeth present between the dentary fang and the symphysis, just as in *Eusthenodon wangsjoi* (from East Greenland), *E.* cf. *wangsjoi*, *Cabonnichthys* (both from Australia), and *Hyneria* (pers. obs.). The genera *Eusthenopteron*, *Mandageria* and *Notorhizodon*

TEXT-FIG. 5. Tristichopteridae gen. nov. et sp. indet., Upper Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 263; isolated right dermopalatine in A, medial view. B, lateral view. C, ventral view. D, dorsal view. Scale bar represents 10 mm.
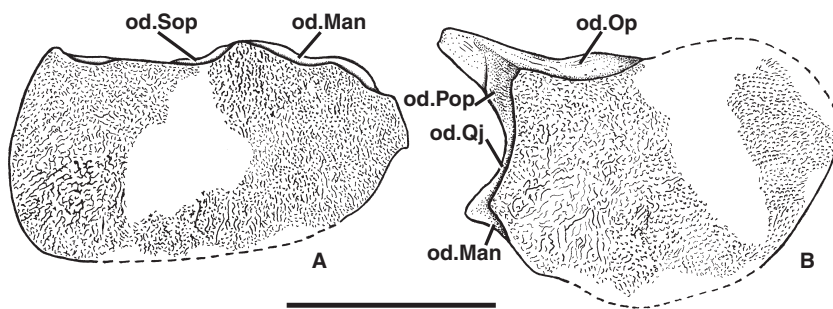
TEXT-FIG. 6. *Langlieria socqueti* gen. nov. et sp. nov., Upper Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 261, right submandibulo-branchiostegal plate A, and MNHN ARD 260, left subopercular B, in lateral views. Scale bar represents 5 cm.

present a marginal dentary dentition extending anteriorly to the symphysis (Johanson 2004). The dentary fang of *Langlieria* is larger than the anterior coronoid fang. Both are laterally flattened in their proximal part.

The parasymphysial region is preserved with a slight distortion due to a lateral compression. The anterior end of the anterior process of the prearticular is not distinguishable from the symphysial area. The dorsal margin of the anterior process of the prearticular is gently concave and ends in an abrupt elevation mesial to the dentary fang. A short, large and smooth furrow is present in front of the end of the anterior process of the prearticular. As supposed by Young *et al.* (1992, fig. 33) in *Notorhizodon*, this furrow could be the attachment area for a parasymphysial dental plate. No rectangular support, as seen in *Eusthenodon* cf. *wangsjoi* from the Famennian of Grenfell, Australia (Johanson 2004, fig. 3A–B), is present in our material. The symphysis area, i.e. the rough area for the contact between the two dentaries, is not well preserved, especially in its posterior part. Nevertheless, the symphysis area appears very reduced in size.

A deep precoronoid fossa is present between the dentary fang and the anterior coronoid. In life this would have received the vomerine fang, as can be seen in an articulated CT-scanned

dentition of *Eusthenopteron* (Ahlberg 2007, 'additional imagery'). The anterior coronoid has a distinct blade-like vertical lamina lateral to the fang pair. In other tristichopterids that possess such a lamina (*Notorhizodon*, Young *et al.* 1992; Johanson 2004; *Eusthenopteron*, pers. obs.) it carries marginal teeth, but in *Langlieria* the teeth are very small, as in *Notorhizodon mackelveyi* from the Givetian of Antarctica (Johanson 2004). By contrast, those tristichopterids that unambiguously lack marginal teeth on the anterior coronoid (*Cabonnichthys*, *Eusthenodon*, probably *Mandageria*) also lack the blade-like vertical lamina (Ahlberg and Johanson 1997). The coronoid fang presents sharp cutting edges. The prearticular is covered with minute tubercles as in *Eusthenodon* and *Cabonnichthys* compared to the larger tubercles seen in *Notorhizodon* (Johanson 2004).

PHYLOGENETIC ANALYSIS

A maximum parsimony analysis of the interrelationships of the Tristichopteridae was performed using the software PAUP* 4.10b (Swofford 1998). Tristichopterid monophyly
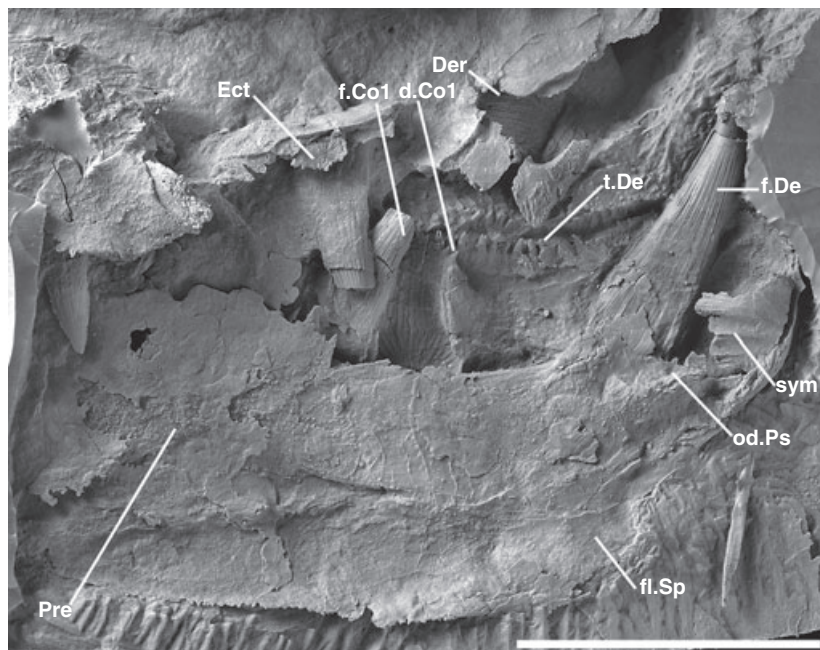
TEXT-FIG. 7. *Langlieria socqueti* gen. nov. et sp. nov., Upper Famennian, Langlier quarry, Durnal, Belgium; MNHN ARD 251; anterior part of the left mandible in medial view with slightly displaced dermopalatine and ectopterygoid. Scale bar represents 5 cm.

Gogonasus

Medoevia

Tristichopterus

Eusthenopteron

Jarvikina

Notorhizodon

Platycephalichthys

Cabonnichthys

Mandageria

Langlieria

Eusthenodon
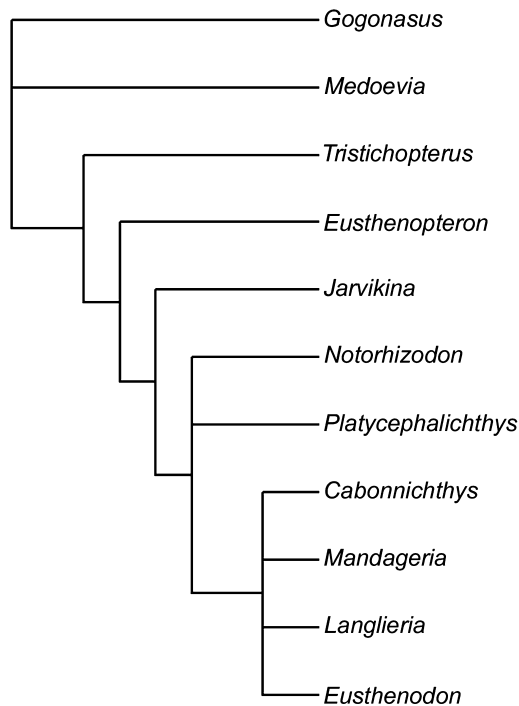
TEXT-FIG. 8. Cladogram showing phylogenetic relationships of the Tristichopteridae including *Langlieria* gen. nov. See Appendix for characters.

has been established in recent studies of tetrapodomorph interrelationships (Ahlberg and Johanson 1998; Snitting 2008). Two 'osteolepidids', *Gogonasus* and *Medoevia*, were chosen as outgroup taxa mainly because they are well known with regard to the characters used here. The data set (11 taxa scored for 22 morphological characters) was small enough to enable the use of the exhaustive search option in PAUP* (see Appendix). All characters were assigned equal weight, and character 15 was defined as ordered multi-state. The result was 12 most parsimonious trees, with a length of 27 steps (CI = 0.852, RI = 0.911, RCI = 0.776), and the strict consensus tree is shown in Text-figure 8. The strict consensus places *Langlieria* in a polychotomy with *Mandageria*, *Eusthenodon* and *Cabonnichthys*, but within this polychotomy there is weak support for a *Mandageria-Eusthenodon* clade excluding *Cabonnichthys* and probably *Langlieria*. *Notorhizodon* and *Platycephalichthys* are joint sister groups to the polychotomy.

DISCUSSION

Langlieria belongs to a globally distributed cohort of large tristichopterids that also includes the cosmopolitan *Eusthenodon* (Jarvik 1952; Lebedev 1992), *Hyneria* from North America (Thomson 1968), *Mandageria* from

Australia (Johanson and Ahlberg 1997), *Notorhizodon* from Antarctica (Young *et al.* 1992) and arguably *Platycephalichthys* (though the monophyly of this remarkably long-lived but geographically restricted genus from the Baltic mid-Frasnian to late Famennian remains to be demonstrated; character codings in the present analysis are based entirely on *Platycephalichthys bischoffi* Voroby-eva 1962). These fishes are all characterised by an elaborate anterior dentition with dentary fangs and, in all except *Platycephalichthys* and possibly *Notorhizodon*, pre-maxillary pseudofangs, as well as a proportionately long ethmosphenoid cranial unit and a body length usually well in excess of 1.5 metres. They belong to a derived clade within the Tristichopteridae (Johanson and Ahlberg 2001, and the phylogeny presented here). We have not been able to include *Hyneria* in our analysis (see Appendix and Text-fig. 8), as there is little published information on its anatomy (Thomson 1968), but personal observation of the extensive unpublished material shows that it has a character complement very similar to *Eusthenodon* and is likely to be the sister taxon of that genus. We will not discuss it at this point.

In addition to these large tristichopterids, the derived clade also contains the much smaller *Cabonnichthys* (Ahlberg and Johanson 1997). *Mandageria* and *Cabonnichthys*, the only members of the clade known from complete bodies, are both characterised by more symmetrical caudal fins and more posteriorly placed median fins than primitive tristichopterids such as *Eusthenopteron* and *Tristichopterus* (Ahlberg and Johanson 1997), suggesting adaptation for motionless hovering and rapid acceleration rather than sustained swimming. Head shape within the derived clade varies from broad (*Hyneria*; pers. obs.) through intermediate (*Cabonnichthys*, *Eusthenodon*; Jarvik 1952; Ahlberg and Johanson 1997) to narrow (*Mandageria*; Johanson and Ahlberg 1997), indicating a degree of ecological separation even among the similar-sized large forms.

Langlieria shows an unusual snout bone pattern with a single anterior median postrostral in contact with the posterior median postrostral (Clément 2002). *Platycephalichthys* (Vorobyeva 1962, 1977) and *Eusthenopteron* (Jarvik 1944, 1980) present more than one anterior median postrostral in contact with the posterior median postrostral and *Eusthenodon wangsjoi* (Jarvik 1952) and *Mandageria* (Johanson and Ahlberg 1997) show more than one anterior median postrostral separated from the posterior median postrostral by nasal bones. The mosaic of bones in the snout region seems to be highly variable within the same species and this feature is probably not of taxonomic value.

In other regards, *Langlieria* presents a combination of derived and primitive tristichopterid characters. The derived characters include a kite-shaped pineal series of bones situated close to the posterior margin of the

parietal shield, dentary fangs, and premaxillary pseudofangs. Primitive characters for the Tristichopteridae include the raised rather than recessed denticulated field of the parasphenoid and the presence of a blade-like vertical lamina on the anterior coronoid. The latter character is particularly significant, as this lamina is absent in *Mandageria*, *Cabonnichthys* and *Eusthenodon*. The ornamentation of the bones is very fine with subparallel ridges on the posterior part of the bones covering the back of the head, similar to *Mandageria*. Possible autapomorphies are the numerous small marginal teeth of the premaxilla and the apparent absence of marginal teeth on the vomer, with the possible exception of its most lateral part.

The revision of the Belgian palaeontology collections has revealed other material of large tristichopterids, some of which may be attributable to *Langlieria*. This includes a large, short and broad postparietal shield (palaeontology collection of Liège University nr 6002) from Modave, Liège Province (Text-figs 9, 10). The postparietal shield, of which only the anterolateral part was previously known (Clément 2002, text-figs 5–6), can now be described from this near-complete specimen lacking only the anterior margin (Text-fig. 10). It is exposed in ventral view, but part of the dorsal surface (Text-fig. 9) shows the same fine *Mandageria*-like ornament as the subopercular. In general appearance the postparietal shield compares well
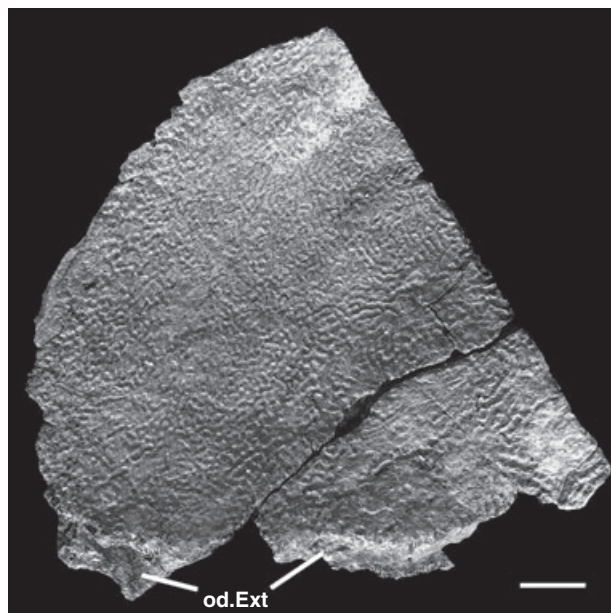
TEXT-FIG. 9. ?*Langlieria socqueti* gen. nov. et sp. nov., Upper Famennian, Modave, Liège province, Belgium; Palaeontology Collection of Liège University nr 6002; left part of a large, short and broad postparietal shield in dorsal view showing the fine bone ornamentation. Same specimen as in Text-figure 10. Scale bar represents 1 cm.

with that of *Eusthenopteron* (Jarvik 1980) and *Platycephalichthys bischoffi* (Vorobyeva 1977, pl. 14, fig. 1), but it is shorter and proportionately wider posteriorly, reminiscent of *Platycephalichthys skuenicus* (Vorobyeva 1977, pl. 14, fig. 2). Supratemporal, tabular and postparietal bones are fused as in large specimens of *Cabonnichthys* and *Mandageria*. The tabular-postparietal sutures are discernable in ventral view (Text-fig. 10) but not in dorsal view (Text-fig. 9). The suture between the two postparietals (also not visible in dorsal view) seems to present a wavy pattern, different from the straight suture, strongly interdigitated in its posterior part, seen in *Platycephalichthys skuenicus* (Vorobyeva 1977, pl. 14, fig. 2). Some internal structures (such as the spiracular lamina or the area for the palatoquadrate dorsal process) are clearly visible but do not provide more information than the anterolateral piece of postparietal shield previously described in Clément (2002, text-figs 5–6).

Part of a very large lower jaw (palaeontology collection of the Royal Institute of Natural Sciences, Brussels, nr I.G. 15.759) from Dison, Liège Province, also shows an ornamentation consisting of very thin anastomosed ridges similar to that of *Langlieria*.

The anterior part of a right lower jaw (palaeontology collection of Liège University nr 6091) figured by Lohest (1888a), and coming from Evieux, Liège Province, most probably also belongs to a tristichopterid. Numerous isolated scales, rounded with an external ornamentation consisting of subparallel undulating ridges and with a boss on the inner side (diagnostic of tristichopterids and rhizodontids) were found in different Famennian localities of Belgium. The tetrapod-bearing locality of Strud, Namur Province, which is currently under investigation, has yielded some large tristichopterid dermal bones. This unexpected richness in large tristichopterid remains in the Upper Devonian of Belgium show the potential for new findings in the future.

The co-occurrence of *Langlieria* and *Eusthenodon* in the Upper Famennian of Durnal quarry (Clément 2002) is noteworthy both from ecological and biogeographical perspectives. While *Langlieria* is so far only known in the Upper Famennian of Belgium, *Eusthenodon* is a cosmopolitan genus that occurs in the Famennian of East Greenland (Jarvik 1952), central Russia (Andreyevka-2 locality in the Tula Region; Alekseev *et al.* 1994; Lebedev 1995), Australia (Grenfell, NSW; Young 1993; Johanson and Ritchie 2000; Johanson 2004, and possibly Eden, Worange Point Formation, NSW; Johanson and Ritchie 2000; Ahlberg *et al.* 2001), South Africa (Witpoort Formation; Gess and Hiller 1995; Anderson *et al.* 1999), and Belgium (Evieux Formation, Clément 2002). *Eusthenodon* is only one of many cosmopolitan genera in the Old Red Sandstone fish faunas of the Upper Devonian; other examples include the lungfish *Soederberghia* which is

TEXT-FIG. 10. ?*Langlieria socqueti* gen. et sp. nov., Upper Famennian, Modave, Liège province, Belgium; Palaeontology Collection of Liège University nr 6002; large, short and broad postparietal shield in ventral view. Scale bar represents 5 cm.
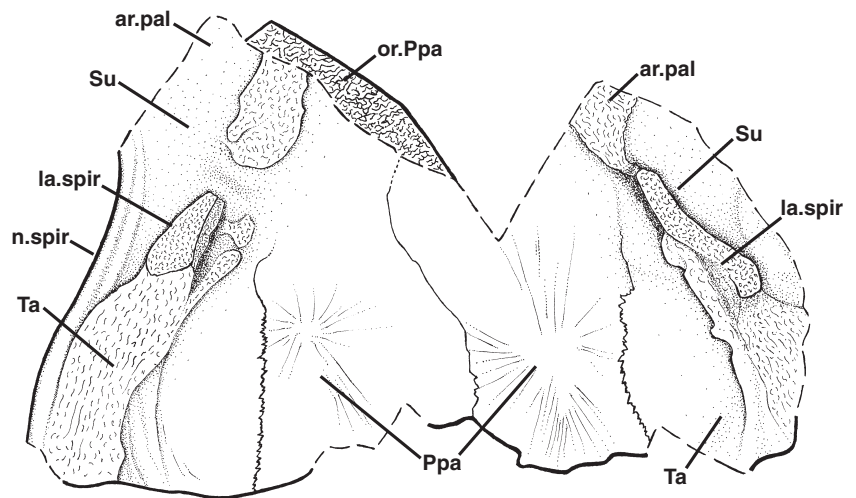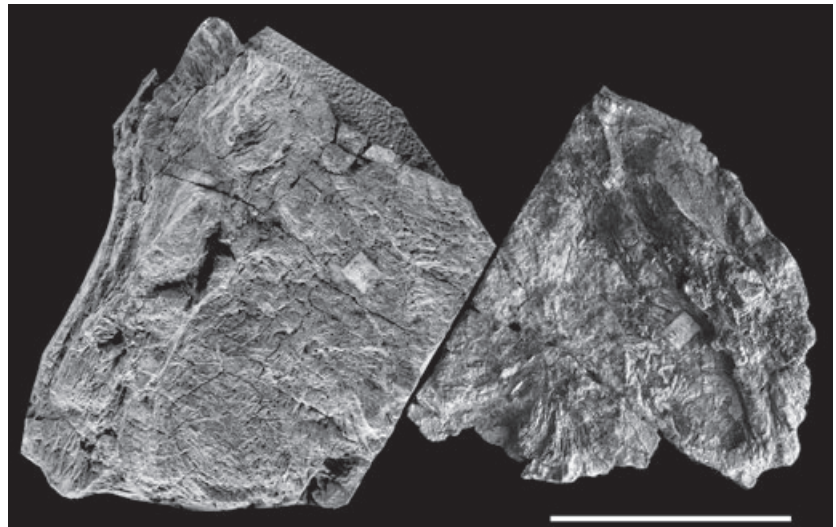
known from Greenland, Belgium, North America and Australia (Ahlberg *et al.* 2001; Clément and Boisvert 2006), the globally distributed antiarch *Bothriolepis*, and the porolepiform *Holoptychius*. It appears that there were few if any significant biogeographical barriers to the spread of these vertebrates. By contrast, the tristichopterids *Langlieria*, *Cabonnichthys*, *Mandageria* and *Hyneria* all appear to have geographically restricted distributions (Thomson 1968; Ahlberg and Johanson 1997), as do all the known Devonian tetrapods (Blieck *et al.* 2007) even though they occur in the same assemblages as the cosmopolitan taxa. If we allow that these apparently restricted genera really are noncosmopolitan, this suggests that the biogeographical barriers controlling their diversification are rather subtle – linked perhaps to specifics of their ecology and mobility rather than to major geographical features such as the distribution of oceans and continents.

Turning to the ecological aspect, Durnal is, to our knowledge, unique as a single locality yielding two distinct but similar-sized tristichopterids. At Canowindra,

NSW, *Mandageria* and *Cabonnichthys* co-occur in the same death assemblage, but *Mandageria* is more than twice as long as *Cabonnichthys* and is also differently proportioned with a narrower head (Ahlberg and Johanson 1997; Johanson and Ahlberg 1997), suggesting that there was a clear ecological separation between the two. In the Catskill Formation, *Eusthenodon* and *Hyneria* have both been recorded, but they do not occur at the same locality (E. B. Daeschler, pers. comm. 2001). At Durnal, on the other hand, *Eusthenodon* and *Langlieria* have been found on the same block of sandstone, so it is clear that they really were contemporaries and do not derive from different levels in the quarry. The morphological differences between the two genera appear to be fairly modest, raising the question of what kind of ecological separation may have allowed the two to coexist.

It is instructive in this context to look at two large predatory Recent teleosts of somewhat tristichopterid-like appearance, the muskellunge (*Esox masquinongy*) and northern pike (*Esox lucius*), which coexist in North

American fresh waters. The two are morphologically similar although the muskellunge is somewhat larger with a maximum length about 125% that of the northern pike. The muskellunge has a somewhat more southerly distribution, but there is extensive overlap between the two species. Comparative ecological studies reveal only minor dietary differences, relating to such parameters as preferred prey size (Wahl and Stein 1993). Interestingly, the northern pike is a cosmopolitan species distributed across the Palearctic and Nearctic, whereas the muskellunge is endemic to North America. Minor ecological differences such as these, which may well be comparable to those that allowed *Langlieria* and *Eusthenodon* to coexist, would almost certainly be impossible to detect in fossil material of the quality seen at Durnal and other Upper Old Red Sandstone localities. In other words, we cannot assume that an absence of evidence for ecological separation in the fossil data equates to a real lack of such separation in life. It is thus the more striking that Upper Old Red Sandstone fossil assemblages containing more than one sarcopterygian normally do show obvious morphological and/or size differences between the taxa present (Ahlberg 1992; Ahlberg and Johanson 1997). This suggests that the ecological separations between the members of UORS faunas were quite substantial.

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APPENDIX

In the list below, reference is given when characters have been introduced in previous published analyses. A&J97: Ahlberg and Johanson 1997, A&J98: Ahlberg and Johanson 1998.

List of characters used in the phylogenetic analysis

1. (Ch. 13, A&J97) Epichordal radials in caudal fin – 0: Absent; 1: Present.

2. (Ch. 2, A&J97) Shape of posterior supraorbital – 0: Posterior process shorter than orbital margin; 1: Posterior process much longer than orbital margin.

3. (Ch. 4, A&J97) Relationship of jugal to orbit – 0: Contributes to orbital margin; 1: Excluded from orbital margin.

4. (Ch. 3, A&J97) Relationship of postorbital to orbit – 0: Contributes to orbital margin; 1: Excluded from orbital margin.

5. (Ch. 1, A&J97) Contact between posterior supraorbital and intertemporal – 0: Present; 1: Absent.

6. (Ch 56, A&J98) Contact between posterior supraorbital and lachrymal – 0: Absent; 1: Present.

7. (Ch. 5, A&J97) Shape of pineal series – 0: Round or oval; 1: Kite-shaped with distinct posterior corner.

8. (Ch. 6, A&J97) Location of pineal foramen or eminence – 0: Level with posterior margin of orbits; 1: Well posterior to orbits.

9. (Ch. 7, A&J97) Enlarged anterior tooth on premaxilla – 0: Absent; 1: Present.

10. (Ch 17, A&J98) Number of fang positions on ectopterygoid – 0: One; 1: Two.

11. (Ch 13, A&J98) Number of fang positions on posterior coronoid – 0: One; 1: Two.

12. (Ch 8, A&J98. Character states redefined here) Coronoid proportions – 0: Posterior coronoid similar in length to middle coronoid; 1: Posterior coronoid significantly longer than middle coronoid.

13. (Ch 11, A&J98) Marginal dentition on dentary reaches lower jaw symphysis – 0: Yes; 1: No.

14. Vertical blade-like lamina present lateral to coronoid fang on anterior coronoid – 0: Yes; 1: No.

15. (Ch. 4, A&J97. Character states redefined here) Shape of caudal fin – 0: Heterocercal; 1: Diphycercal; 2: Rhomboidal.

16. Accessory vomers – 0: Absent; 1: Present.

17. Cutting edges on fangs – 0: Absent; 1: Present.

18. Location of posterior point of median postrostral – 0: Anterior to orbits; 1: Level with or posterior to orbits.

19. Marginal tooth row anterior to dermopalatine fang – 0: Present; 1: Absent.

20. (Ch. 10, A&J97. Character states redefined here) Marginal teeth present on all coronoids – 0: Yes; 1: No.

21. (Ch. 11, A&J97) Dentary fang – 0: Absent; 1: Present.

22. (Ch. 12, A&J97) Postspiracular: 0: Absent; 1: Present.

Character-taxon matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Gogonasus	?	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0	0	1	0	0	0	0
Medoevia	?	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	0	0
Cabonnichthys	1	1	0	1	0	0	1	1	1	1	1	1	1	1	2	1	1	0	0	1	1	1
Eusthenodon	?	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	1	1	?	1	1	1
Eusthenopteron	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1
Jarvikina	?	1	0	0	0	0	0	1	0	?	1	?	0	0	?	0	0	0	?	0	0	1
Langlieria	?	?	?	?	?	?	1	1	1	1	?	?	1	0	?	?	1	1	1	?	1	1
Mandageria	1	1	1	1	1	1	1	1	1	1	1	1	0	1	2	1	1	1	1	1	1	1
Notorhizodon	?	?	?	?	?	?	?	?	?	1	1	1	0	0	?	?	0	?	?	0	1	1
Platycephalichthys	?	1	1	1	?	?	1	1	0	?	1	1	0	0	?	0	0	0	?	0	1	1
Tristichopterus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1