

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

by GAËL CLEMENT*, DANIEL SNITTING* and PER ERIK AHLBERG*

*Subdepartment of Evolutionary Organismal Biology, Department of Physiology and Developmental Biology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18A, 752 36 Uppsala, Sweden; e-mails: per.ahlberg@ebc.uu.se; daniel.snitting@ebc.uu.se

Muséum national d'Histoire naturelle (MNHN), Département Histoire de la Terre, CNRS-UMR 7207 Pale'obiodiversité et Pale'oenvironnements, 57 rue Cuvier, CP38, 75005 Paris, France; e-mail: gclement@mnhn.fr

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: 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 sub-mandibulo-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 (Clement 2002) marked the beginning of revision of the Devonian vertebrate palaeontology collections of the main institutions of Belgium (Liege 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 1888a, 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 (Lelieuvre 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 (Bleick and Lelieuvre 1995; Cloutier and et Candilier 1995; Derycke 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 Liege 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 Clement 2005), a rhynchodipterid lungfish (Clement and Boisvert 2006) and an *Ichthyostega*-like tetrapod (Clement et al. 2004). Some other sarcopterygians are still under study (dipnoans, possible megalichthyids, rhizodontids, osteolepidids) and will be described in separate papers.

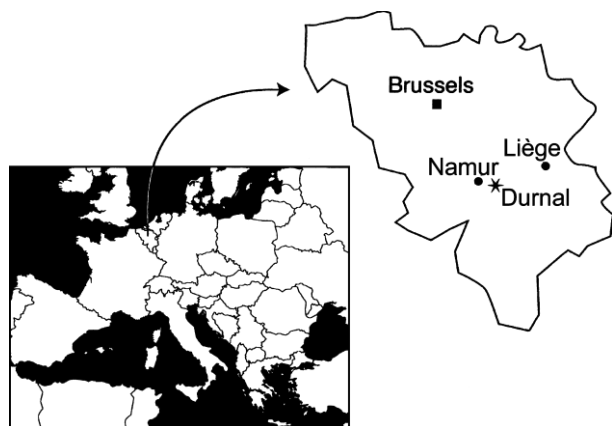
The diversity and abundance of vertebrate fossil remains (mostly placoderms and sarcopterygians) already

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) (Blick 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 wangsjoii* 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 as describe this large tristichopterid fish 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 pre-maxillae (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

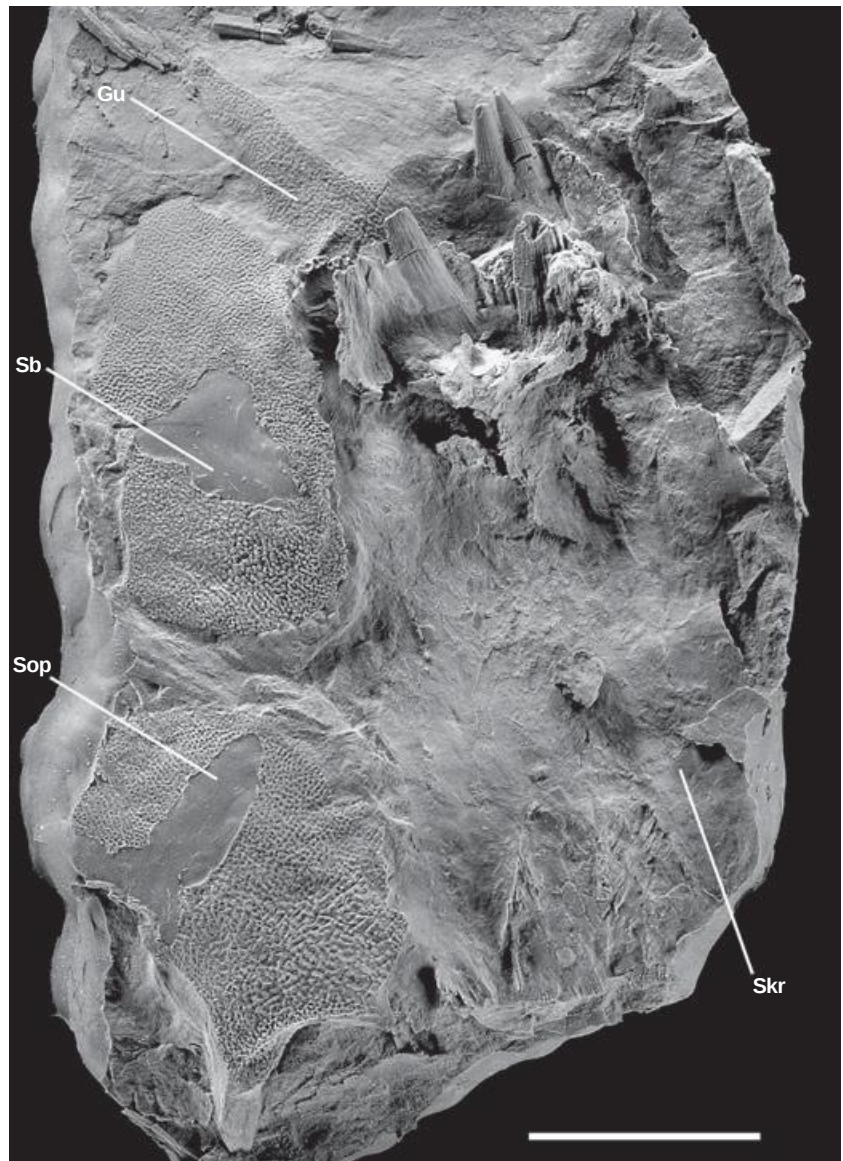
The Langlier quarry is situated in the northern part of the Dinant synclinorium, south of the London-Brabant Massif in an outcrop of the Evieux Formation of the upper Famennian 'Condroz Sandstones' sequence. According to Goemaere (1995), the Evieux Formation is characterised by an alternation of micaceous 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.

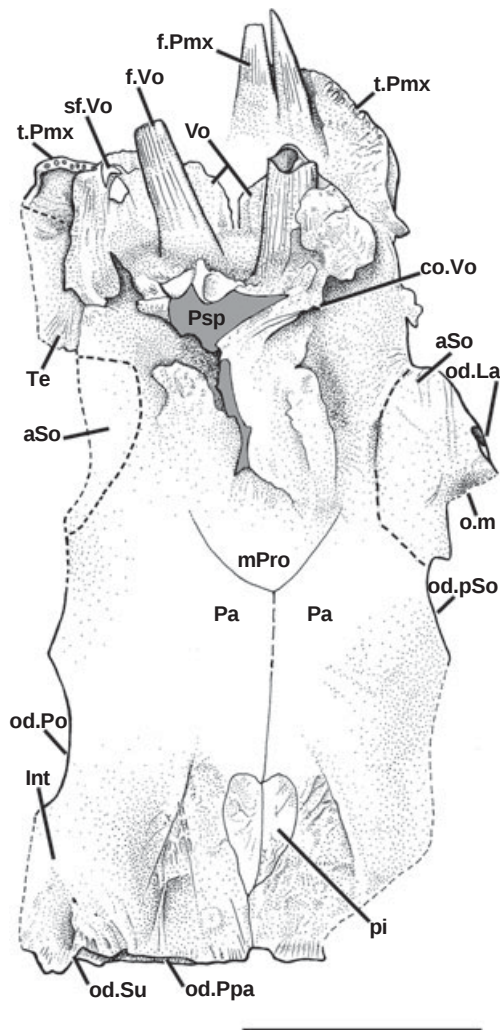
Anatomical abbreviations. ant.pr, anterior process of the dermopalatine; ar.pal, area for the palatoquadrate dorsal process (paratemporal process); aSo, anterior supraorbital bone;

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, symphyseal 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 PALAEOLOGY

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.

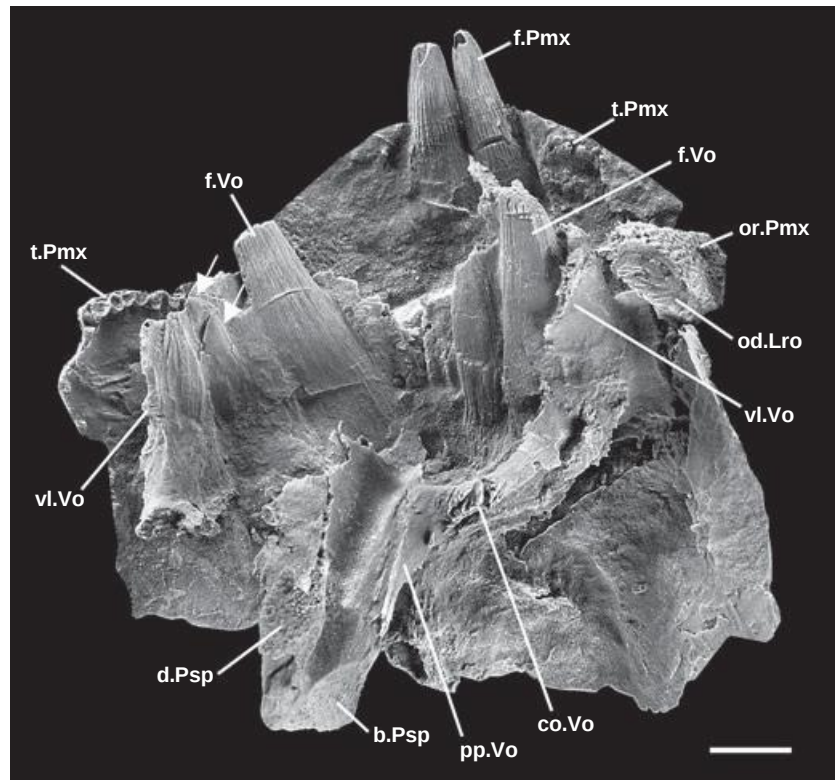
Primitive. Denticulated field on parasphenoid stands proud of the body of the bone, forming a distinct 'prow' anteriorly, rather than being recessed into the body of the bone; raised marginal crest present on anterior coronoid; round, thin, moderately large scales.

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 wangsjo* 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 Clement (2002, fig. 7).

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