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## TRISTICHOPTERIDS (SARCOPTERYGII, TETRAPODOMORPHA) FROM THE UPPER DEVONIAN TETRAPOD-BEARING LOCALITY OF STRUD (BELGIUM, UPPER FAMENNIAN), WITH PHYLOGENETIC AND PALEO BIOGEOGRAPHIC CONSIDERATIONS

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**ABSTRACT**—We describe new material of the tristichopterids cf. *Langlieria socqueti* and cf. *Eusthenodon wangsjoii* and other unassignable tetrapodomorph remains from the upper Famennian locality of Strud, Belgium. Because of recent improvements in our tristichopterid knowledge, a new phylogenetic analysis is presented in addition to a paleobiogeographic analysis using the Bayesian binary Markov chain Monte Carlo (MCMC) statistical method. The origin of the whole tristichopterid clade is reconstructed with a very likely western European origin. Much of the early tristichopterid history took place in Euramerica. During the Late Devonian, tristichopterids most probably spread from Euramerica into Gondwana. The highly nested tristichopterid clade formed by *Cabonnichthys burnsi*, *Mandageria fairfaxi*, *E. wangsjoii*, *Edenopteron keithcrooki*, and *Hyneria lindae* most likely differentiated in Australia. Then dispersal events occurred from Australia to Euramerica with *Hyneria lindae* (to eastern North America) and *E. wangsjoii* (to Greenland/western Europe). The latter dispersal events, during the Famennian, are in agreement with the Great Devonian Interchange, which predicts dispersal events between Gondwana and Euramerica at this time.

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

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### INTRODUCTION

Tristichopteridae is a clade of fusiform, aquatic sarcopterygians with an extratemporal bone located between opercular and lateral extrascapular bones (Ahlberg and Johanson, 1997; Johanson and Ahlberg, 1997; Snitting, 2008a). Scales are devoid of cosmine, rounded, and thin, with a small median boss on the internal surface. The caudal fin is trifurcate in nested forms (Cloutier and Ahlberg, 1996).

Tristichopterids are known from the Middle Devonian (latest Givetian; Egerton, 1861; Young et al., 1992; Swartz, 2012) through the Upper Devonian (Famennian; Jarvik, 1952; Clément, 2002; Clément et al., 2009). Their (presumed) adult body sizes ranged from 30 cm to several meters in length. These lobe-finned predatory vertebrates are quite common in the Devonian vertebrate assemblages of the world, with about 20 described

species, but only the species *Eusthenodon wangsjoii* (often incorrectly written as ‘wängsjöi’; Snitting and Blom, 2009) has been found in several remote countries (Greenland and Belgium; Jarvik, 1952; Clément, 2002; Blom et al., 2007; Clément et al., 2009). The presence of this genus in Australia (Johanson, 2004), eastern Europe (Alekseev et al., 1994; Lebedev, 1995), and South Africa (Gess and Hiller, 1995) has been evoked, but the specific assignment (and sometimes the generic one) is not certain. The report of *Eusthenodon wangsjoii* in the Upper Catskill Formation in Pennsylvania, U.S.A. (Thomson, 1976), has been recently overturned by Daeschler and Downs (2018). Otherwise, unassignable tristichopterid remains are known from Morocco (Lehman, 1977; Lelièvre and Janvier, 1986; Lelièvre et al., 1993), from Colombia (Janvier and Maisey, 2010; Olive et al., 2019), and probably from Iran (Davesne et al., 2015).

Several studies have been done on tristichopterids from Belgium (Lohest, 1888; Cloutier and Candilier, 1995; Clément, 2002; Clément et al., 2009; Olive et al., 2015b). *Eusthenodon wangsjoii* and *Langlieria socqueti* were described from Durnal, Namur Province (Clément, 2002; Clément et al., 2009); cf. *Langlieria* from Dison and Modave, Liège Province (Clément et al.,

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2009); and unassignable tristichopterid scales from Becco, Liège Province (Olive et al., 2015b). Tristichopterid remains have also been reported from the localities of Strud, Namur Province (Clément et al., 2009; Denayer et al., 2016:table 1), and Evieux, Liège Province (Clément et al., 2009).

We report here on new tristichopterid material from the tetrapod-bearing locality of Strud. We also provide a new phylogenetic analysis that was prompted by recent improvements in our knowledge of tristichopterid diversity (Schultze and Reed, 2012; Swartz, 2012; Young et al., 2013, 2019; Borgen and Nakrem, 2016; Daeschler and Downs, 2018; Downs et al., 2018; Daeschler et al., 2019). We use our resulting cladogram as the basis for a study of the paleobiogeographic history of Tristichopteridae.

**Institutional Abbreviations**—**IRSNB**, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; **MNHN**, Muséum national d'Histoire naturelle, Paris, France.

**Anatomical Abbreviations**—**a.ad.**, anterior wall of adductor fossa; **ar.hyo.**, articulation area with hyomandibular; **ar.pal.**, area for palatoquadrate dorsal process (paratemporal process); **aut.p.**, autopalatine process; **bu.**, bulge; **cl.m.**, cleithrum mesial crest; **co.1.**, anterior coronoid; **co.2.**, middle coronoid; **co.3.**, posterior coronoid; **d.**, dentary; **d.d.**, dentary marginal dentition; **d.f.**, dentary fang; **d.s.**, dentary suture; **ent.pa.**, anterior process of entopterygoid; **f.co.1.**, anterior coronoid fang; **f.co.2.**, middle coronoid fang; **f.co.3.**, posterior coronoid fang; **fl.co.3.**, anterior fang of posterior coronoid; **f2.co.3.**, second fang of posterior coronoid; **f3.co.3.**, posterior fang of posterior coronoid; **fo.ico.**, intercoronoid fossa; **fo.pco.**, precoronoid fossa; **inf.1–4.**, infradentaries 1–4; **la.l.**, lateral vertical lamina; **la.m.**, mesial vertical lamina; **l.d.**, dorsal lamina of cleithrum; **l.pb.**, postbranchial lamina of dorsal blade of cleithrum; **l.v.**, ventral lamina of cleithrum; **m.ad.**, posterior part forming the mesial part of the adductor fossa; **md.g.**, mandibular sensory groove; **o.r.**, oblique ridge; **ov.ano.**, area of cleithrum overlapping anocleithrum; **ov.br.**, branchial operculum overlapping area; **ov.cla.**, clavicle overlapping area; **ov.it.**, intertemporal overlapping area; **ov.j.**, jugal overlapping area; **ov.l.ext.**, lateral extrascapular overlapping area; **ov.mx.**, maxilla overlapping area; **ov.p.sr.**, posterior supraorbital overlapping area; **ov.po.**, post-orbital overlapping area; **ov.pop.**, preopercular overlapping area; **ov.psp.**, postspiracular overlapping area; **ov.qj.**, quadratojugal overlapping area; **ov.sm1.**, submandibular 1 overlapping area; **ov.sq.**, squamosal overlapping area; **ov.st.**, supratemporal overlapping area; **ov.ta.**, tabular overlapping area; **p.g.**, parietal sensory groove; **pi.**, pineal area; **pop.g.**, preopercular sensory groove; **ppr.**, posterior process of postorbital; **pra.**, anterior process; **pr.ad.**, anterodorsal process; **r.f.**, replacement pit of middle coronoid fang; **ri.ioc.**, ridge housing infraorbital sensory canal; **ri.it.so.**, ridge dividing intertemporal and postorbital overlapping areas; **sp.n.**, spiracular notch.

## GEOLOGICAL SETTING

During the late Famennian, what is now Belgium was located along the southeastern margin of Euramerica (London-Brabant Peninsula; Ziegler, 1990). In Wallonia, southern Belgium, Devonian outcrops are present in the Dinant Synclinorium (allochthonous), Veldre Area, Theux Tectonic Window, Brabant Parautochthon, and Haine-Sambre-Meuse Overturned Thrust Sheets (HSM OTS; Fig. 1). These Variscan structures form the Namur-Dinant Basin, which developed during Devonian and Carboniferous times (Thorez et al., 2006). Famennian outcrops from Belgium show a regressive trend from shales formed in an open marine environment (Famenne Group, early Famennian) to fluviolagunal siltstones, sandstones, and dolomites (Evieux Formation, upper Famennian) (Thorez and Dreesen, 1986). Upper Famennian deposits from HSM OTS, Veldre Area, and Theux Tectonic Window are more proximal, and the fluviolagunal facies are generally better developed than in contemporary

deposits from the Dinant Synclinorium (Thorez et al., 2006). The strata at Strud belong to the HSM OTS. Tristichopterid remains were found in beds A, B, D–D', and E of lithological unit 7 (Fig. 1). Lithological unit 7 belongs to the upper Famennian Evieux Formation. The sedimentology of this unit corresponds to the filling sequence of a channel in an alluvial plain (Denayer et al., 2016).

## MATERIALS AND METHODS

### Preparation and Imaging

All specimens were mechanically prepared except for a few specimens that were virtually observed by conventional X-ray tomography at the AST-RX (Accès Scientifique à la Tomographie à Rayons X) facility of the MNHN. Scanning parameters were as follows: voltage = 85 kV, current = 260  $\mu$ A; for IRSNB P 9918, number of slices = 3000, voxel size = 0.029 mm. IRSNB P 9919 is included in three rock blocks that were scanned independently. IRSNB P 9919a, number of slices = 1500, voxel size = 0.098 mm; IRSNB P 9919b, number of slices = 2000, voxel size = 0.098 mm; IRSNB P 9919c, number of slices = 1800, voxel size = 0.116 mm. IRSNB P 9918 and IRSNB P 9919 were virtually segmented with MIMICS (Materialise Interactive Medical Image Control System) 16.0 (Materialise Inc.; proprietary software at the MNHN) at the Atelier 3D, Centre de Recherche en Paléontologie–Paris, MNHN.

### Phylogenetic Analysis

Ahlberg and Johanson (1997) generated a phylogenetic analysis of Tristichopteridae that has served as a starting point for subsequent analyses focusing on the clade (e.g., Clément et al., 2009) or focusing on a broader scale than the clade, i.e., osteolepiformes (e.g., Johanson and Ahlberg, 2001; Snitting, 2008b; Swartz, 2012). The phylogenetic study developed for the present paper considers 15 species and is the first published analysis to include *Hyneria lindae*, *Edenopteron keithcrooki*, *Langlieria radiatus*, and *Eusthenopteron jenkinsi*. We chose to perform a species-level analysis because we did not want to assume that the genera are monophyletic. The analysis used 26 morphological characters (Appendix S1 in Supplemental Data 1). Twenty characters come directly or are modified from previous analyses (Ahlberg and Johanson, 1997, 1998; Snitting, 2008a; Clément et al., 2009), and six new characters (21–26) are introduced here. In an effort to minimize qualitative assessments in character scoring, we included only characters with well-defined states. We checked character scores against published descriptions and figures, as well as original material for *H. lindae*, *Eusthenopteron jenkinsi*, *L. radiatus*, and *Langlieria socqueti*.

The parsimony analysis was performed through the branch-and-bound search algorithm of PAUP 4.0a162 (Swofford, 2002) on the complete matrix (Appendix S2 in Supplemental Data 1). All characters were assigned equal weight, and only characters 9, 24, and 26 were defined as multistate. All characters were unordered, except for characters 9 and 24, which are considered to be morphoclines. We chose *Gogonasmus andrewsae* and *Spodichthys buetleri* as outgroups because they are well known and phylogenetically close to tristichopterids (Long, 1985a; Long et al., 2006; Snitting, 2008b; Holland and Long, 2009). We calculated Bremer indices for each node to indicate the node robustness. Details of the parsimony analysis, and notably the character-state changes, are available in Appendix S3 in Supplemental Data 1. Appendix S4 in Supplemental Data 1 displays the list of synapomorphies at each node.

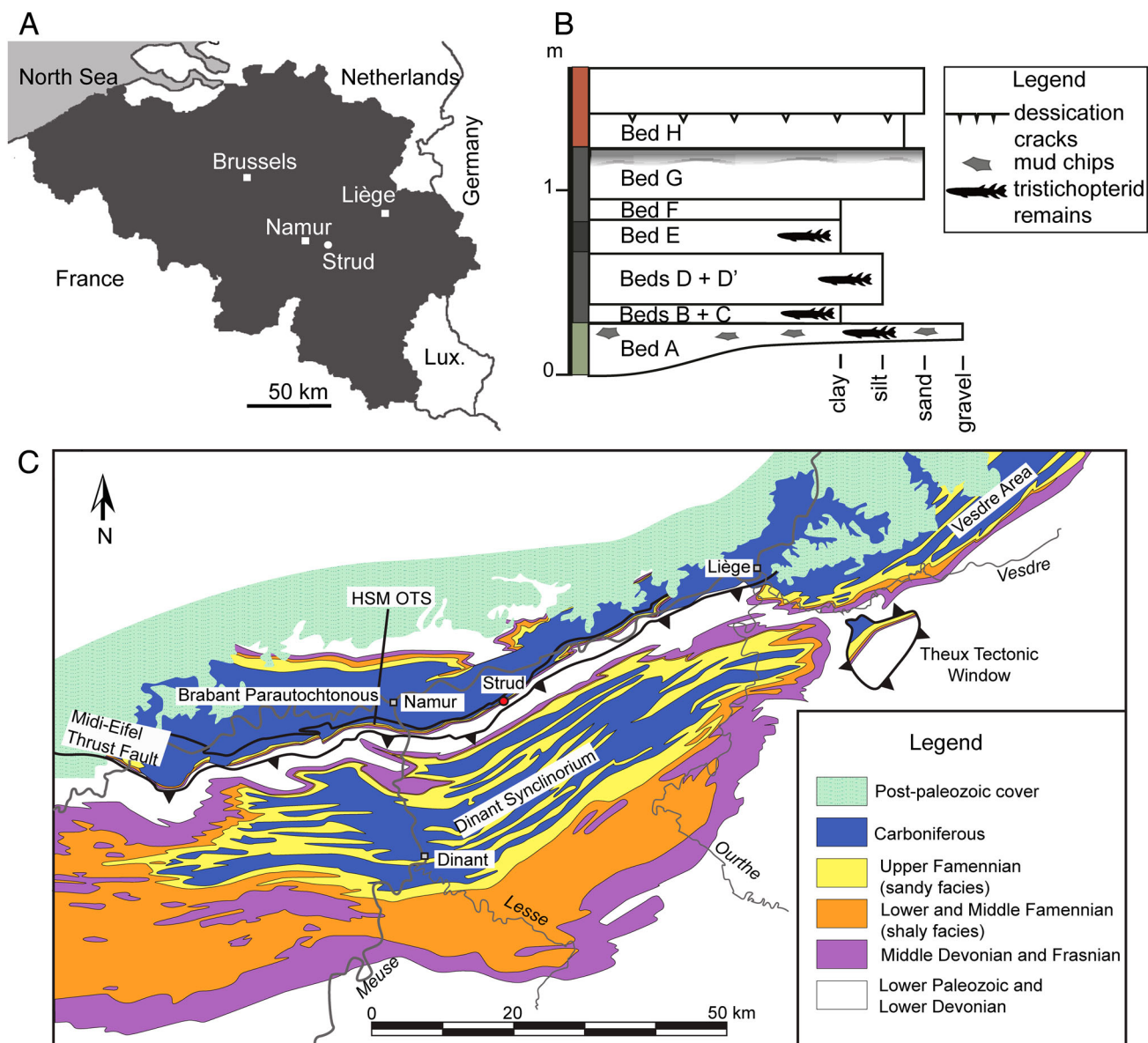


FIGURE 1. Geographic and geological localizations of the Strud locality, Namur Province, Belgium. **A**, geographic map. **B**, schematic block diagram of the Strud channel with the location of tristichopterid remains, modified from Denayer et al (2016). **C**, geological map of southern Belgium, modified from Denayer et al. (2016), redrawn from Béthune (1954).

### Historical Biogeography Analysis

A historical biogeography analysis was performed using Bayesian binary Markov chain Monte Carlo (BBM), in RASP 3.1 (Yu et al., 2015). This is a statistical method that uses Bayesian inference to reconstruct the ancestral state or biogeographic origin of clades (Ronquist and Huelsenbeck, 2003). We applied BBM on the 60% majority-rule consensus tree resulting from the parsimony analysis. Nine geographic areas were designated (Australia, Greenland, Eastern Canada, Northern Canada, Pennsylvania, Nevada, Western Europe, Eastern Europe/Russia, and Antarctica), and each taxon was assigned to the geographic area(s) where it was found (Fig. 2; Appendix S5 in Supplemental Data 1). The geographic categories were made according to the Late Devonian paleogeography proposed by

Scotese (2014) and Ziegler (1990). For instance, Scotland, England, and Belgium were all parts of the Rhenish Basin during the Late Devonian (Ziegler, 1990) and thus were grouped together as ‘Western Europe.’ The BBM analysis was performed over  $10^6$  generations with 10 Markov chains, sampling every 100 generations, with the temperature set to 0.1. It is noteworthy that we also performed a regular Markov chain Monte Carlo (MCMC) sampling analysis without heating (i.e., MC = 1) and the results were identical. The first 100 trees were discarded as part of the burn-in period, and the Jukes-Cantor model was used, with equal among-site rate variation. The results of the biogeographic reconstructions for each node are presented in Appendix S6 in Supplemental Data 1. The results of the analysis are expressed as the probability of a given clade originating from each of nine continental areas.

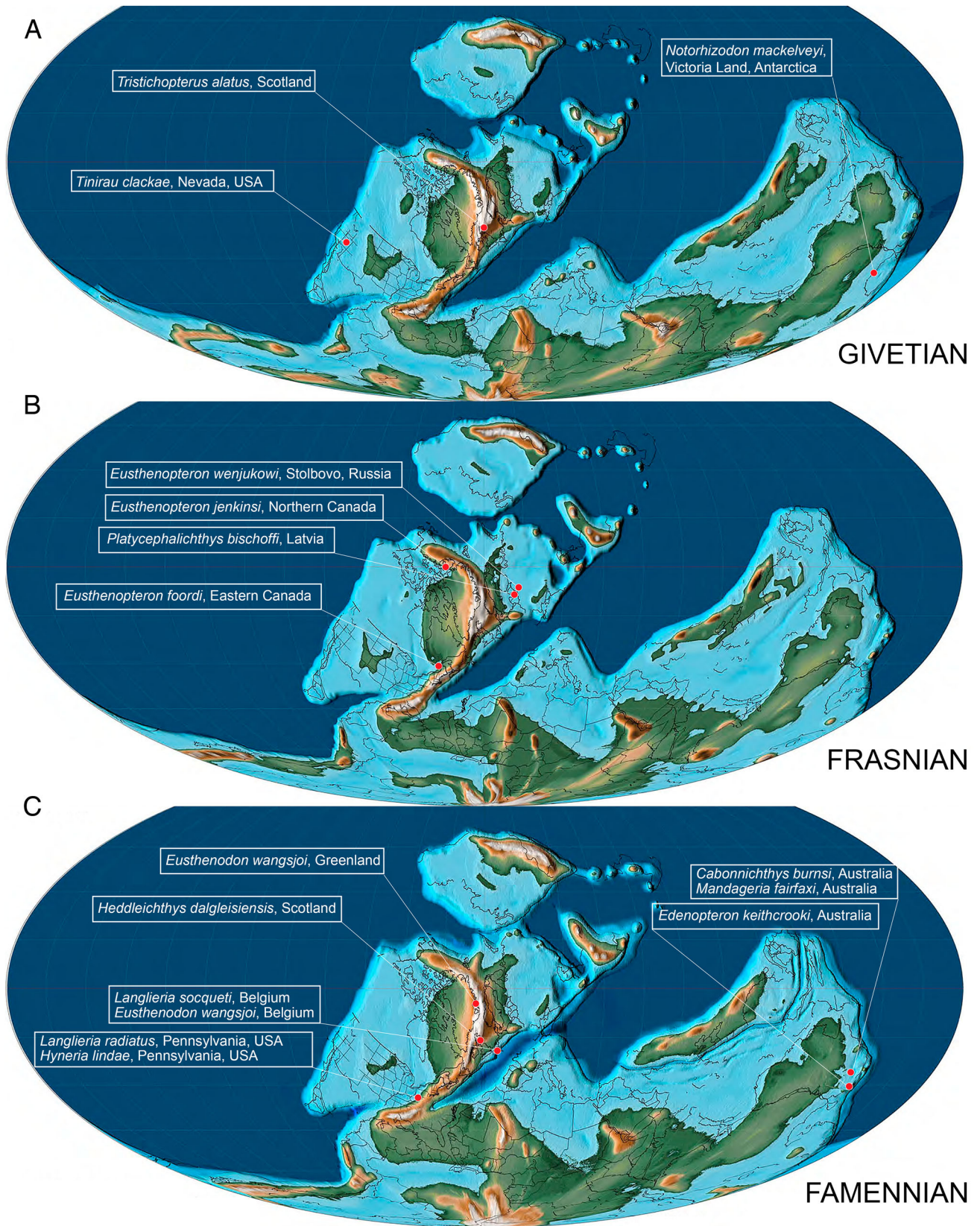


FIGURE 2. Paleogeographic maps of the **A**, Givetian, **B**, Frasnian, and **C**, Famennian showing the worldwide distribution of tristichopterids. Tristichopterid localities have been indicated according to the outlines of continents as they are nowadays. The large scaling of the maps does not permit observation of regional details. Maps from Scotese (2014).

## SYSTEMATIC PALEONTOLOGY

SARCOPTERYGII Romer, 1955

OSTEOLEPIFORMES Berg, 1937

TRISTICHOPTERIDAE Cope, 1887

cf. *LANGLIERIA* Clément, Snitting, and Ahlberg, 2009**Type Species**—*Langlieria socqueti* Clément, Snitting, and Ahlberg, 2009.cf. *LANGLIERIA SOCQUETI* Clément, Snitting, and Ahlberg, 2009 (Fig. 3)**Referred Material**—IRSNB P 9912, partial left squamosal (bone has been mechanically removed to have access to the mould of the external surface); IRSNB P 9913, right mandibular ramus.**Locality and Horizon**—Strud quarry, Namur Province, Belgium, Evieux Formation, upper Famennian, Upper Devonian.**Remarks**—Two tristichopterid species have been described from Belgium: *Eusthenodon wangsjoii* and *Langlieria socqueti*. We assign the following material, isolated squamosal and lower jaw, to cf. *L. socqueti* according to dermal ornament and size category. Of the two specimens described here, only one (IRSNB P 9913) exhibits a feature included in the diagnostic character combination of Clément et al. (2009), and this feature (presence of dentary fang pair) is present in most tristichopterids. The one autapomorphy that Clément et al. (2009) cite for *L. socqueti* (absence of marginal vomerine teeth; Clément et al., 2009) is impossible to observe in the new material.**Description****Squamosal**—The squamosal (IRSNB P 9912; Fig. 3A–C) exhibits a prominent rostradorsal process and a less prominent rostromedial process. The dorsal margin of the bone is concave, and the dorsocaudal corner is rounded and located well rostral to the caudoventral portion of the squamosal. The dermal surface of the squamosal contains wide, conjoined areas for the overlap of the postorbital and jugal bones. There is a narrow area for the overlapping maxilla along the ventral margin. The relationship between the squamosal and the maxilla is reversed in IRSNB P 9912 relative to the condition in a partial skull of *Langlieria socqueti* (MNHN ARD 250) from the type locality (squamosal overlaps maxilla; Clément, 2002:figs. 8, 9). The maxilla overlap onto the squamosal is the most common condition in Tristichopteridae; the reversed condition is otherwise known only in *Eusthenodon wangsjoii* and possibly *Platycephalichthys bischoffi* (Clément, 2002). On the visceral surface of IRSNB P 9912, along the dorsal margin, there is an elongated and narrow area of overlap onto the supratemporal, the tabular, and possibly the postspiracular.**Lower Jaw**—The dentary (IRSNB P 9913; Fig. 3D–F) displays a large fang pair with cutting edges and ridges on its base. Ridges are absent or not preserved on the apex. As in MNHN ARD 251 (Clément et al., 2009: fig. 7), there is no marginal dentition of the dentary labial to the fangs or between the fangs and the mandibular symphysis. Among tristichopterids, a marginal dentary tooth row that appears only distal to the fangs is additionally observed in *Cabonichthys burnsi* (Johanson and Ahlberg, 1997), *Edenopteron keithcrooki* (Young et al., 2013), and *E. wangsjoii* (Jarvik, 1952; Johanson, 2004).

The distal end of infradentary 4 in IRSNB P 9913 shows a wide and ventrally slanting area of overlap for the quadratojugal. Ventral to the quadratojugal overlap area is a long eroded mandibular groove. The overlapping area for the first submandibular

can be observed on the ventral part of infradentary 1 (IRSNB P 9913; Fig. 3D–E).

Only one fang of coronoid 3 is visible in IRSNB P 9913 (Fig. 3D–F). The number of fang pairs on coronoid 3 is impossible to determine in this specimen, and the condition is unknown in *L. socqueti*. Among tristichopterids, only *Spodichthys buetleri* (Snitting, 2008b), *Tristichopterus alatus* (Snitting, 2009), and *Ed. keithcrooki* (Young et al., 2013) are reported with one fang pair, rather than two, on coronoid 3. The coronoid fangs of IRSNB P 9913 exhibit cutting edges and striations at the base that may or may not reach the apex of the tooth.**Dermatocranial Ornament**—The dermatocranial ornament of IRSNB P 9912 and IRSNB P 9913 is very fine. IRSNB P 9912 (squamosal) exhibits subparallel ridges in the rostradorsal part of the bone and anastomosing ridges elsewhere. On IRSNB P 9913 (dentary + infradentaries), the ornament is mainly made of smooth anastomosed ridges, which are more strongly pronounced at the distal end of the dentary.cf. *EUSTHENODON* Jarvik, 1952**Type Species**—*Eusthenodon wangsjoii* Jarvik, 1952.cf. *EUSTHENODON WANGSJOII* Jarvik, 1952 (Figs. 4–5)**Referred Material**—IRSNB P 9910, partial left parietal; IRSNB P 9914, left supratemporal, part and counterpart; IRSNB P 9915, partial left postorbital; IRSNB P 9916, left preopercular; IRSNB P 9917, left opercular; IRSNB P 9918, right dentary; IRSNB P 9919, partial right mandible.**Locality and Horizon**—Strud quarry, Namur Province, Belgium, Evieux Formation, upper Famennian, Upper Devonian.**Remarks**—These specimens are referred to cf. *Eusthenodon wangsjoii* on account of dermal ornament and size category. In addition, IRSNB P 9915 (postorbital) shares general shape characteristics as well as a well-developed rostradorsal process (Jarvik, 1952:pl. 9) with the *Eusthenodon wangsjoii* holotype. IRSNB P 9917 (preopercular) has a wide rostromedial process similar to that observed in the *E. wangsjoii* holotype (Jarvik, 1952:pl. 10). General shape characteristics are shared between IRSNB P 9914 (supratemporal) and IRSNB P 9918 (opercular) and the *E. wangsjoii* holotype (Jarvik, 1952:pl. 9). IRSNB P 9919 (mandible) shares a lack of fusion among the dermal mandibular bones with the *E. wangsjoii* holotype (Jarvik, 1952:pl. 10).**Description****Parietal**—IRSNB P 9910 (Fig. 4E, F) is an isolated partial parietal that preserves much of the caudal and medial margins. The dermal surface of the parietal exhibits a short area of supratemporal overlap along the caudolateral margin. The posterior oblique pitline groove is observed lateral to the pineal region. The shape of the parietal suggests a kite-shaped pineal series, contrary to the teardrop-shaped condition in the *E. wangsjoii* holotype (Jarvik, 1952:pl. 9) and in Clément's (2002) emended diagnosis of the species. In addition, it appears as though the pineal series either reaches or nearly reaches the caudal margin of the parietal shield. Several specimens of *E. wangsjoii* (including the holotype, Jarvik, 1952:pl. 9) show a more rostrally positioned pineal series. High variability of pineal positioning in *E. wangsjoii* has previously been recognized by Jarvik (1985).**Supratemporal/Tabular**—IRSNB P 9914 (Fig. 4A–D) represents a fused supratemporal and tabular. The spiracular notch is strongly hook-shaped, as observed in the *E. wangsjoii* original material (P. 1479; Jarvik, 1952:pl. 11, fig. 1). Areas overlapped by the intertemporal and the postorbital are observed on the

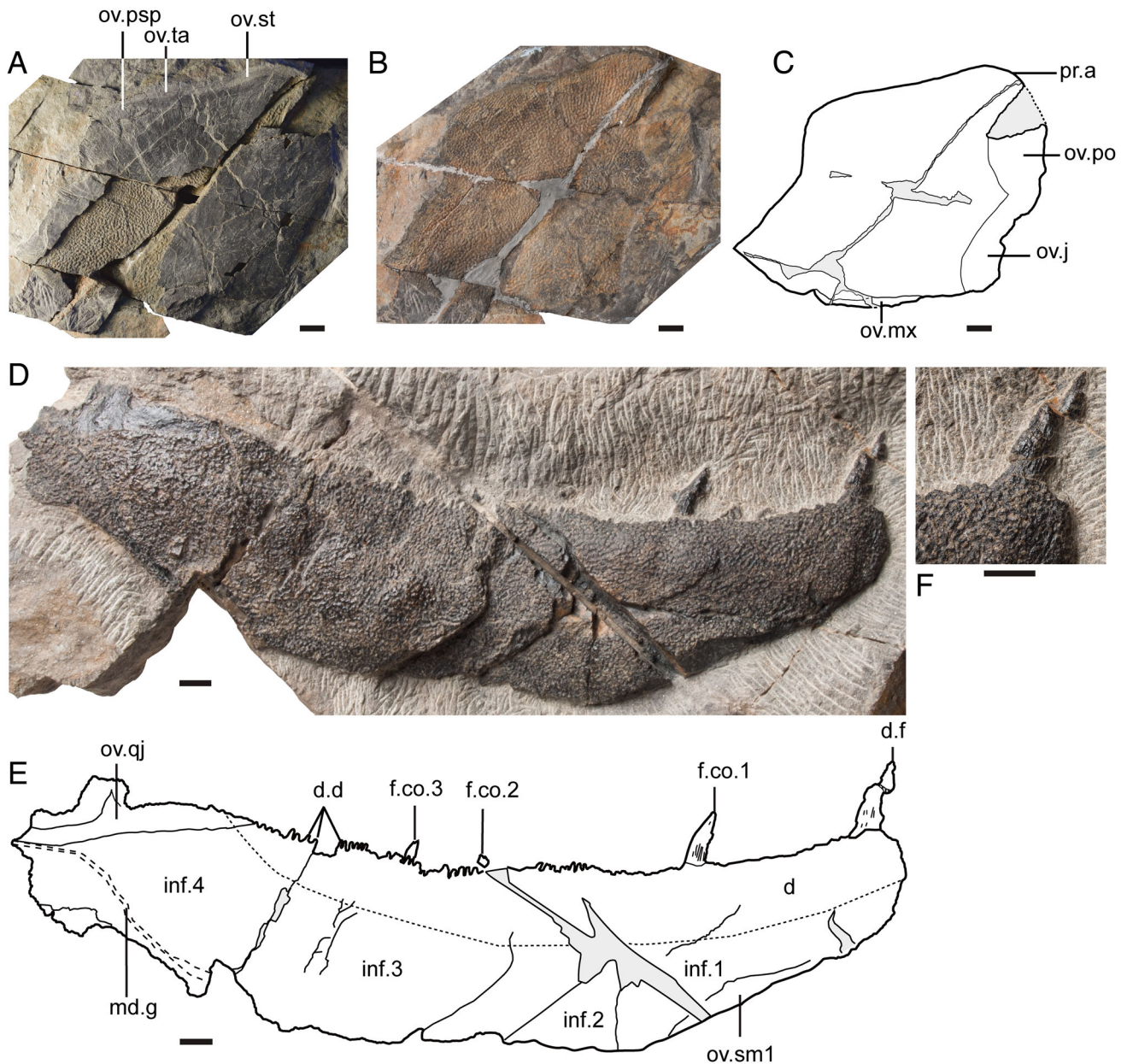


FIGURE 3. cf. *Langlieria socqueti*, Strud, Belgium, upper Famennian. **A–C**, IRSNB P 9912, left squamosal: **A**, photograph of internal view; **B**, photograph of imprint of the external surface (bone removed); **C**, interpretive drawing of external view. **D–F**, IRSNB P 9913, right mandibular ramus, external view: **D**, photograph; **E**, interpretive drawing; **F**, close-up photograph of the symphysis. Scale bars equal 1 cm.

dermal surface of the supratermporal (Fig. 4A), in the rostralateral corner. A strong ridge divides the two overlap areas (Fig. 4C) as in *Langlieria socqueti* (Clément, 2002:fig. 6b). On the visceral surface, a smooth depression is visible anteriorly. This depression may have received the palatoquadrate paratemporal process (as proposed by Clément, 2002, for *E. wangsjoii*). The ridge housing the infraorbital canal is present around this depression. A possible articulation area with the hyomandibula is located in the caudomedial corner (Fig. 4D).

**Postorbital**—IRSNB P 9915 (Fig. 4G–H) is an isolated partial postorbital with an extended shared area for the overlap of both intertemporal and posterior supraorbital bones. These overlap areas are not observable in the *E. wangsjoii* type material.

**Preopercular**—IRSNB P 9916 (Fig. 4I–J) is a partial left preopercular that preserves an area for squamosal overlap that appears short but may be incomplete.

**Opercular**—IRSNB P 9917 (Fig. 4K–L) is an opercular with a high height/length ratio (1.5). Jarvik (1952) described the opercular of *E. wangsjoii* as higher than long and figures a single specimen (P. 1481; Jarvik, 1952:pl. 12:2) with a ratio that is not as high (= 1.24) as that in IRSNB P 9917. The ventral margin of IRSNB P 9917 is rounded as in *Eusthenopteron foordi* (e.g., Jarvik, 1944a) and is notably unlike the condition in *Cabonnichthys burnsi* (Ahlberg and Johanson, 1997:fig. 3), where the margin is indented by the subopercular. The dorsal margin of IRSNB P 9917 shows a well-developed and large overlap area divided into two parts by a ridge. The larger rostral part was

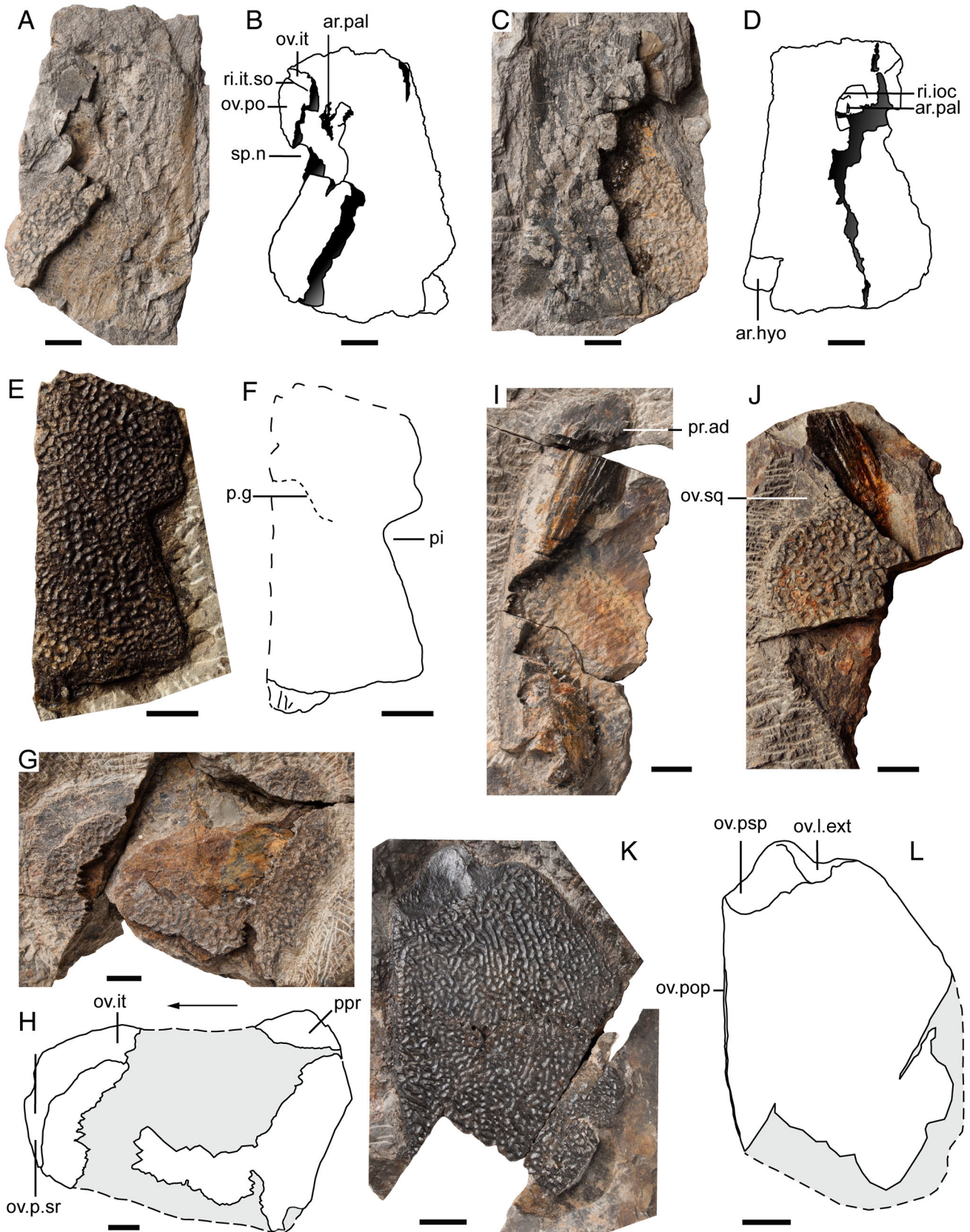


FIGURE 4. cf. *Eusthenodon wangsjoii*, Strud, Belgium, upper Famennian. **A–D**, IRSNB P 9914, left supratergital and left tabular: **A**, photograph and **B**, interpretive drawing of external view; **C**, photograph and **D**, interpretive drawing of visceral view. **E, F**, IRSNB P 9910, incomplete left parietal: **E**, photograph and **F**, interpretive drawing of external view. **G, H**, IRSNB P 9915, left postorbital: **G**, photograph and **H**, interpretive drawing of external view. **I, J**, IRSNB P 9916, left preopercular, photographs of **I**, external and **J**, visceral views. **K, L**, IRSNB P 9917, left opercular, **K**, photograph and **L**, interpretive drawing of external view. Black arrow points to anterior. Scale bars equal 1 cm (**A–H**) and 2 cm (**I–L**).



probably for the postspiracular bone and the smaller caudal part for the lateral extrascapular. In *E. wangsjoii*, only the overlap area for the postspiracular has been previously reported (by Jarvik, 1952:pl. 12:2). However, Jarvik (1952:64) expresses doubt over whether the area was overlapped by the postspiracular or the lateral extrascapular. The rostral margin of IRSNB P 9917 displays a very narrow overlap area for the preopercular.

**Lower Jaw**—IRSNB P 9918 (Fig. 5A–B) exhibits a dentary fang pair, and no marginal teeth are observed from the fang pair to the symphysis. Within Tristichopteridae, this condition is shared among *C. burnsi* (Johanson and Ahlberg, 1997), *Ed. keithcrooki* (Young et al., 2013), *E. wangsjoii* (Jarvik, 1952; Johanson, 2004), *Langlieria socqueti* (Clément et al., 2009), and cf. *L. socqueti* (this paper). IRSNB P 9919 (Fig. 5D–F) includes all three coronoids. Coronoid 3 is much longer than coronoids 1 and 2. Among tristichopterids, only *S. buetleri* (Snitting, 2009) and *T. alatus* (Snitting, 2009) have been reported with a third coronoid of a length subequal to that of coronoids 1 and 2. The fangs of coronoids 1 and 2 have sharp carinae along the mesial and distal margins. The fangs of both pairs on coronoid 3 are much smaller than those of coronoids 1 and 2. No striations are visible on the coronoid fangs of IRSNB P 9919. A marginal tooth row is not visible on any of the three coronoids of IRSNB P 9919. This may be a result of preservation; no other tristichopterid is entirely without marginal coronoid dentition. Among tristichopterids, the most reduced condition previously recognized (marginal teeth on third coronoid only) is observed in *E. wangsjoii* (Jarvik, 1952), *Hyneria lindae* (Daeschler and Downs, 2018), and *Mandageria fairfaxi* (Johanson and Ahlberg, 1997).

**Dermatocranial Ornament**—As described in Clément's (2002) emended diagnosis for *E. wangsjoii*, the dermatocranial ornament of these Strud specimens consists of ridges forming distinct networks and independent tubercles are rare.

#### DESCRIPTION OF OTHER TRISTICHOPTERID MATERIAL FROM STRUD

Unless otherwise noted, the specimens reported below are referred to cf. Tristichopteridae, sp. indet., based on shapes, sizes, and dermal ornaments that compare more favorably to the Strud tristichopterids than to the other vertebrates at the locality (acanthodians, actinopterygians, antiarchs, arthrodires, phyllolepid, porolepiforms, rhizodonts, osteolepidids, dipnoans, tetrapods; Lohest, 1888; Leriche, 1931; Clément et al., 2004; Clément and Boisvert; 2006; Olive, 2015; Olive et al., 2015a, 2016a, 2016b). Absence of diagnostic features prevents more specific taxonomic assignments. Taxonomic caution is especially warranted in the cases of isolated tetrapodomorph cleithra and suboperculars. Several authors have reported on the intraspecific variability of cleithrum morphology and ornament and of subopercular morphology in tetrapodomorphs (Andrews and Westoll, 1970; Jarvik, 1944b). For many of the specimens presented here, very little meaningful anatomical description is possible. Our intention then is to simply present an inventory of potential tristichopterid material produced by recent collecting efforts at the Strud locality.

IRSNB P 9920 (Fig. 6A) is a right preopercular with a deep dorsoventral sensory groove in its caudal half. Its ornamentation comprises small tubercles and ridges.

IRSNB P 9921–9923 (Fig. 6B–D) are isolated subopercular bones. The rostral process of IRSNB P 9921 is especially long and rod-like (Fig. 6B). IRSNB P 9923 is much smaller than the other two and has a more rounded shape with a short, stout rostral process (Fig. 6D).

IRSNB P 9911 (Fig. 6E, F) is a partial right entopterygoid and palatoquadrate. Much of the preserved entopterygoid is without denticles, although this is possibly due to weathering. A large

and rounded oblique ridge is present in the middle of the bone. This ridge runs caudodorsally and broadens from a prominent rounded bulge (Fig. 6F). The rostral end of the specimen exhibits a pronounced autopalatine process and a ventral process of the entopterygoid, with a short triangular groove between them that tapers caudally. A prominent ascending process is partially observed at the dorsal preservational limit. A row of large and pointed denticles appear along the ventral margin of the rostral end of the entopterygoid. The ventral margin of the palatoquadrate is relatively straight and does not exhibit the wide lateral flange that surrounds the caudal end of the ectopterygoid in *Eusthenodon wangsjoii* (Jarvik, 1952:pl. 16:2).

IRSNB P 9924 and IRSNB P 9927 are isolated cleithra. The dorsal lamina ornament of IRSNB P 9924 (Fig. 7A, B) is a network of generally parallel fine anastomosed crests; that of IRSNB P 9927 (Fig. 7C) is coarse tubercles and small ridges similar to the cleithrum ornament of *Platycephalichthys bischoffi* (Vorobyeva, 1959, 1962) and *Langlieria socqueti* (Clément, 2002; Clément et al., 2009).

IRSNB P 9928 and IRSNB P 9929 (Fig. 7D, E) are isolated fangs with ridges along their base and sharp carinae along the mesial and distal edges.

IRSNB P 9925–9926 and 9930–9931 (Fig. 7F–I) are isolated scales. Each shows the visceral boss that allows an assignment to Tristichopteridae, sp. indet. Several (IRSNB P 9930–9931, IRSNB P 9926) show radiating grooves on the free margin.

## RESULTS

### Phylogenetic Analysis

The parsimony analysis of the complete data matrix yielded 49 most parsimonious trees with a score of 58 (consistency index [CI] = 0.5; retention index [RI] = 0.66; rescaled consistency index [RCI] = 0.33). Figure 8 presents the 60% majority-rule consensus tree (length [L] = 59; CI = 0.49; RI = 0.65; RCI = 0.32) that was generated from the data. Bremer indices (Bremer, 1988) are very low (0 or 1; see the strict consensus tree in Fig. S1 in Supplemental Data 1), which means that our results are poorly supported and need to be discussed cautiously. Here, we will only describe the clades by their unambiguous synapomorphies (see Appendix S4 in Supplemental Data 1 for more details).

Usually considered to be a tristichopterid, *Tristichopterus alatus* has the most basal position in the resulting cladogram.

The monophyletic ingroup (node 11) is defined by one unambiguous synapomorphy: presence of an extratemporal in a postspiracular position (character 19, state 1). Two ambiguous synapomorphies also support this clade (both Acctran and Deltran optimizations, because of the polytomy in the outgroup): premaxillary teeth closest to the symphysis gradually increase in size (9,1), and less than half of the lacrimal rostral to the orbit (25,1). In our analysis, in accordance with Borgen and Nakrem (2016), the ancestral character state for the premaxillary dentition (character 9) is homodonty (morphotype A, state 0).

Node 10 is characterized by two unambiguous synapomorphies: two fangs on posterior coronoid (11,1), and posterior coronoid significantly longer than middle coronoid (12,1).

Node 9 is characterized by three unambiguous synapomorphies: a posterior process of the posterior supraorbital much longer than its orbital margin (6,1), pineal foramen well posterior to the orbits (8,1), and maxilla does not overlap onto squamosal (23,1).

*Eusthenopteron wenjukowi* and *Tinirau clackae* (node 1, collapsed in the strict consensus tree; Appendix S3 in Supplemental Data 1) share one unambiguous synapomorphy: a constant height of the maxilla (24,2).

Node 8 (collapsed in the strict consensus tree; Appendix S3 in Supplemental Data 1) is defined by three unambiguous

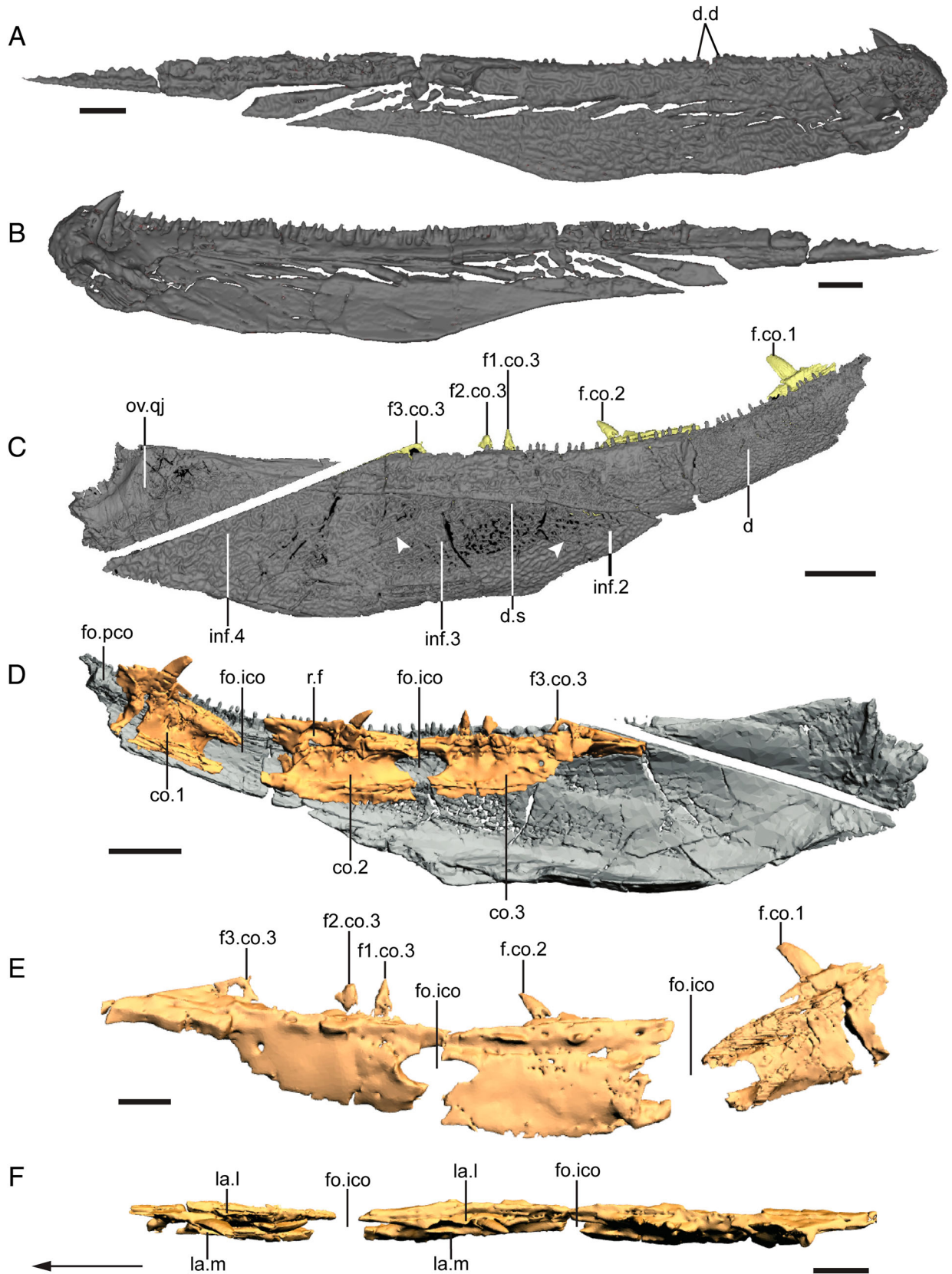


FIGURE 5. cf. *Eusthenodon wangsjoii*, Strud, Belgium, upper Famennian. **A, B**, IRSNB P 9918, right dentary, digital renderings of **A**, external and **B**, visceral views. **C, D**, IRSNB P 9919, right mandible, digital renderings of **C**, external and **D**, visceral views. **E, F**, IRSNB P 9919, coronoids, digital renderings of **E**, external and **F**, apical views. Left white arrowhead indicates putative suture between the infradentaries 3 and 4; right white arrowhead indicates pit line of infradentary 2. Black arrow points anteriorly. Scale bars equal 1 cm (**A, B, E, F**) and 2 cm (**C, D**).

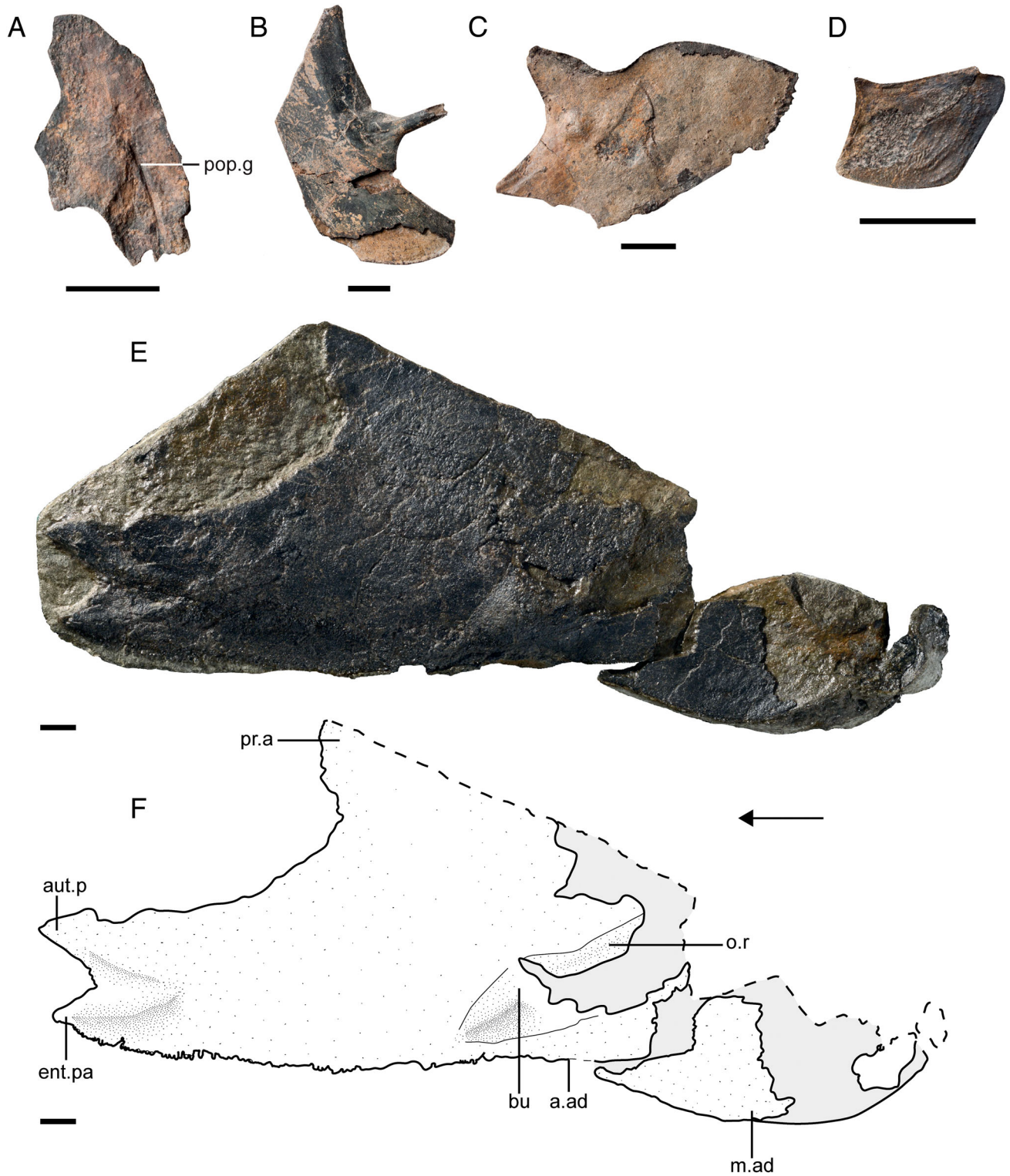


FIGURE 6. cf. Tristichopteridae indet., Strud, Belgium, upper Famennian. **A**, IRSNB P 9920, right preopercular, photograph of external view. **B**, IRSNB P 9921, left subopercular, photograph of visceral view. **C**, IRSNB P 9922, left subopercular, photograph of visceral view. **D**, IRSNB P 9923, left subopercular, photograph of visceral view. **E**, **F**, IRSNB P 9911, right palatoquadrate: **E**, photograph and **F**, interpretative drawing of visceral view. Black arrow points anteriorly. Scale bars equal 1 cm.

synapomorphies: a symmetrical caudal fin (2,1), a kite or teardrop-shaped pineal area (7,1), and the presence of a dentary fang pair (17,1).

The Famennian clade (node 7) is characterized by one unambiguous synapomorphy: absence of contact between the marginal dentition of the dentary and the lower jaw symphysis (13,1).

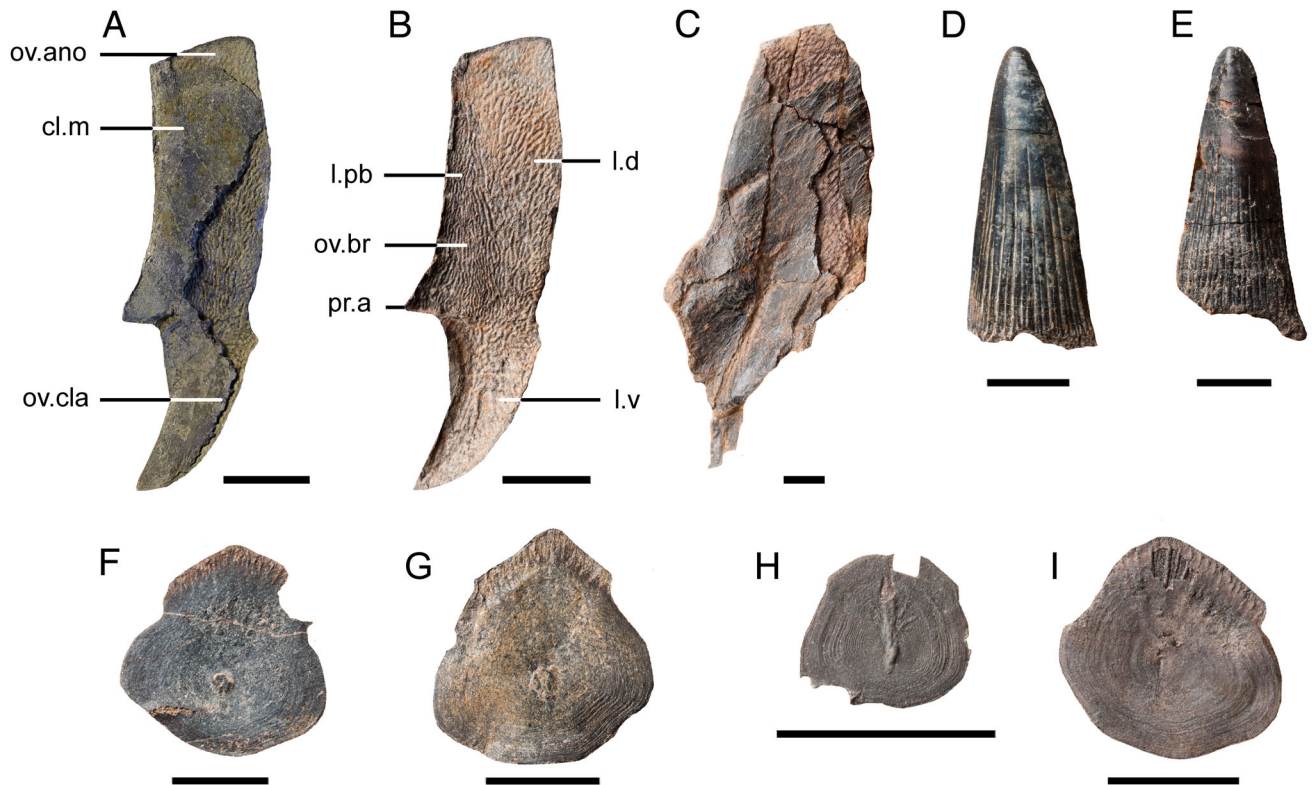


FIGURE 7. cf. Tristichopteridae indet., Strud, Belgium, upper Famennian. **A,B**, IRSNB P 9924, right cleithrum, in **A**, visceral view and **B**, imprint of the external view (bone removed). **C**, IRSNB P 9927, incomplete right cleithrum, visceral view. **D**, IRSNB P 9928, isolated fang, photograph of labial or lingual view. **E**, IRSNB P 9929, isolated fang, photograph of labial or lingual view. **F**, IRSNB P 9930, isolated scale, visceral view. **G**, IRSNB P 9931, isolated scale, visceral view. **H**, IRSNB P 9925, isolated scale, visceral view. **I**, IRSNB P 9926, isolated scale, visceral view. Scale bars equal 1 cm.

Taxa of node 6 share one unambiguous synapomorphy: absence of a vertical blade-like lamina lateral to the coronoid fang on the anterior coronoid (14,1).

Node 5 is supported by two synapomorphies: presence of accessory vomers (15,1), and lateral margin of posterior process of vomer displaying a distinct corner (18,0).

The clade gathering *Mandageria fairfaxi*, *Eusthenodon wangsjoji*, *Edenopteron keithcrooki*, and *Hynieria lindae* (node 4) is characterized by three unambiguous synapomorphies: jugal excluded from orbital margin (3,1), absence of contact between posterior supraorbital and intertemporal (5,1), and half or more of the lacrimal rostral to the orbit (25,0).

Node 3 is characterized by two unambiguous synapomorphies: denticulated field of parasphenoid, which is recessed into the body of the parasphenoid (20,1), and maximum height of maxilla at lacrimal-jugal junction (24,1).

*Edenopteron keithcrooki* and *H. lindae* (node 2) share two unambiguous synapomorphies: width/length ratio of vomers + parasphenoid equal or more than 0.5 (21,0), and width/length ratio of parietals equal or more than 0.5 (22,1).

### Historical Biogeography Analysis

Here, we will only consider the posterior probabilities of geographic origins for the ingroup, because the two outgroups cannot establish whether the ancestral geographic area is Australia (*Gogonasus andrewsae*) or Greenland (*Spodichthys buetleri*). This is also why we choose to represent the parsimony tree with a basal polytomy.

The monophyletic ingroup Tristichopteridae is most probably of western Europe origin (with ~74% probability), which is mainly due to the basal position of *Tristichopterus alatus* (Fig. 8).

Clade 7 includes the most nested tristichopterids: *Langlieria socqueti*, *Langlieria radiatus*, *Cabonnichthys burnsi*, *Mandageria fairfaxi*, *Eusthenodon wangsjoji*, *Edenopteron keithcrooki*, and *Hynieria lindae*. This clade has most likely a western Europe origin (~94% probability).

An Australian origin is highly probable for the clade gathering *C. burnsi*, *M. fairfaxi*, and *E. wangsjoji* (clade 5, with ~97% probability) and the clade including *Ed. keithcrooki* and *H. lindae* (clade 2, with ~89% probability).

## DISCUSSION

### Phylogenetic Analysis

Most recent phylogenetic analyses of tristichopterids support a highly nested clade of tristichopterids including variably *Cabonnichthys*, *Eusthenodon*, *Mandageria*, and *Langlieria socqueti* (Ahlberg and Johanson, 1997, 1998; Johanson and Ahlberg, 2001; Zhu and Ahlberg, 2004; Snitting, 2008b; Clément et al., 2009; Swartz, 2012). The present analysis gathers the same taxa (node 7) and additionally includes *Langlieria radiatus*, *Hynieria lindae*, and *Edenopteron keithcrooki*, the three being included for the first time in a published phylogenetic analysis (Fig. 8).

**Position of *Spodichthys***—*Spodichthys buetleri* is the sister taxon to all tristichopterids in all phylogenetic analyses where it is included (Snitting, 2008a, 2008b). It displays a number of plesiomorphic characters such as the presence of contact between the posterior supraorbital and the intertemporal (5,1), the

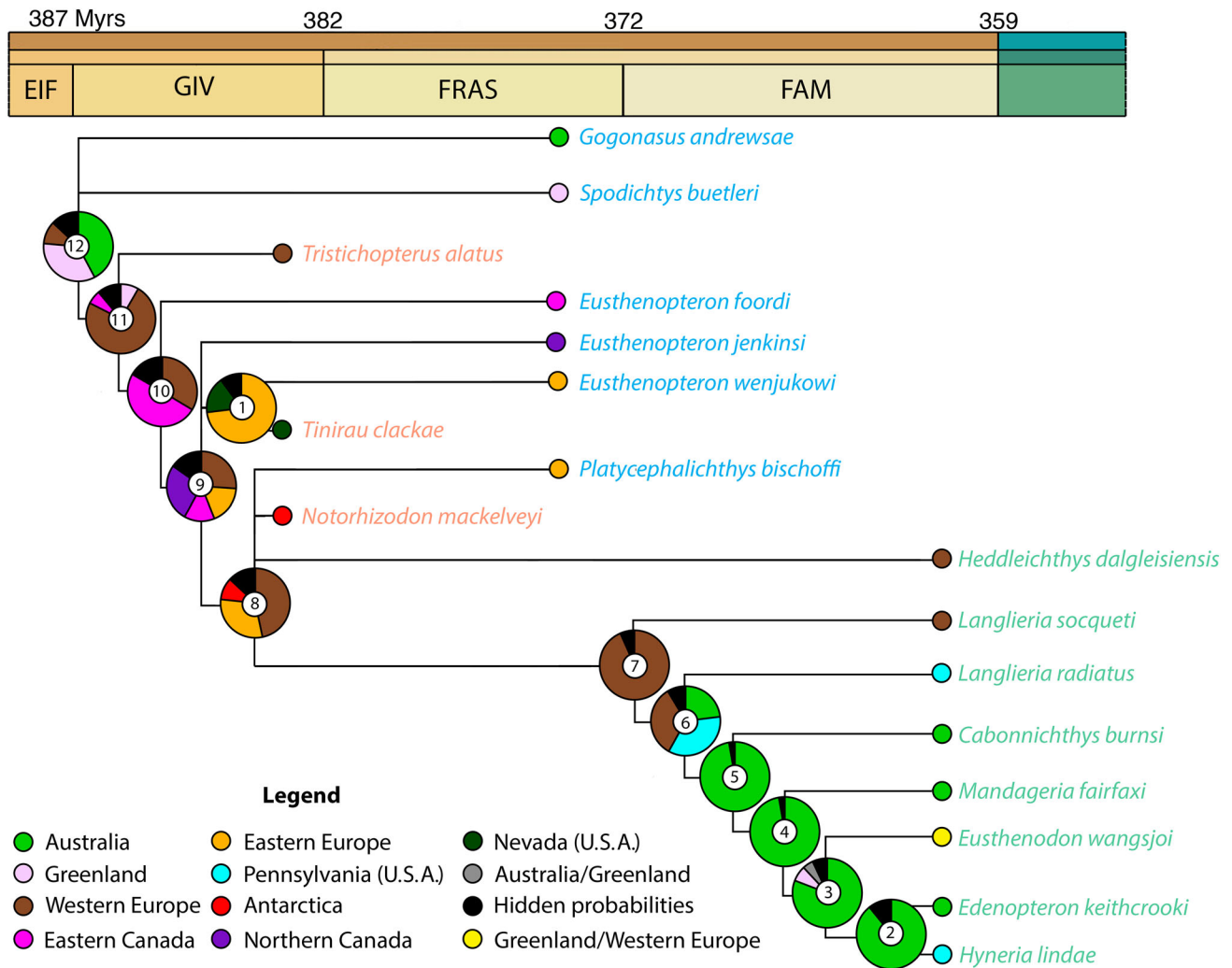


FIGURE 8. The 60% majority-rule consensus tree resulting from the parsimony analysis and showing the phylogenetic relationships of the Tristichopteridae, with the results of the Bayesian binary MCMC analysis mapped on. The number in the center of each pie chart corresponds to the node number. The pie chart over each node represents the probability that the clade originated from each continental area. ‘Hidden probabilities’ corresponds to ranges with probabilities less than 5%, which are hidden and lumped together. Givetian taxa in orange, Frasnian in blue, and Famennian in green. **Abbreviations:** EIF, Eifelian; FAM, Famennian; FRAS, Frasnian; GIV, Givetian.

pineal foramen located at the level with or anterior to the posterior margin of the orbit (8,0), only one fang position on the ectopterygoid and the third coronoid (10,0 and 11,0), a posterior coronoid similar in length to the middle coronoid (12,0), the presence of a vertical lamina lateral to the coronoid fang on the anterior coronoid (14,0), or the absence of a dentary fang pair (17,0). The phylogenetic position of *S. buetleri* remains an open question because more than half of the characters are missing data (15 of 26). One diagnostic character of Tristichopteridae, the extratemporal reaching into the postspiracular area, has never been observed in *S. buetleri*; hence, its exclusion from the clade and its sister-group relationship to it (Snitting, 2008b).

**Monophyly of Tristichopteridae**—Tristichopterid monophyly has been established in several studies (Long, 1985b; Ahlberg and Johanson, 1997, 1998; Johanson and Ahlberg, 2001; Zhu and Ahlberg, 2004; Snitting, 2008a, 2008b; Clément et al., 2009) and rejected in some others (e.g., Lu et al., 2012; Swartz, 2012). In Zhu et al. (2017), tristichopterids form a clade in the strict consensus tree, but in the maximum clade credibility tree from the

Bayesian analysis, tetrapods and elpistostegalids have been found nested within tristichopterids. This paraphyly is due to the inclusion of *Marsdenichthys* in the tristichopterid group. We chose not to include it in the present analysis because it is often recovered as a non-tristichopterid in several analyses (e.g., Long et al., 2006; Swartz, 2012). The presence of an extratemporal in a postspiracular position (19,1) is a synapomorphy of the clade Tristichopteridae (the extratemporal is not in a postspiracular position in *Marsdenichthys*; Long, 1985b; Holland et al., 2010). For this character, we scored *Tinirau clackae* ‘1’, contrary to Swartz (2012), because the extratemporal clearly extends along the posterior half of the lateral margin of the tabular and along approximately the anterior 25% of the lateral margin of the lateral extrascapular in Swartz (2012:fig. s4).

**Newly Added Taxa**—*Edenopteron keithcrooki*, *H. lindae*, *Eusthenopteron jenkinsi*, and *L. radiatus* are included in a phylogenetic analysis for the first time. The first two appear as sister species to one another (node 2) and form the clade of the most highly nested tristichopterids. Node 2 is supported by two

unambiguous and three ambiguous synapomorphies (see Results and Appendix S4 in Supplemental Data 1).

The position of *H. lindae* within tristichopterids is highly nested, as previously suggested by several authors (Daeschler and Shubin, 2007; Clément et al., 2009; Daeschler and Downs, 2018). Daeschler and Downs (2018) proposed a highly nested phylogenetic position for *H. lindae* due to a suite of derived characters that includes contact between the parietal and the postorbital, a postorbital that does not contribute to the orbital margin, a wide and concave denticulated plate of the parasphenoid, a dentary fang pair, and a lack of marginal dentition on all but the third coronoid. The present phylogenetic analysis supports all of these as either (1) derived features appearing quite early in the history of tristichopterids (dentary fang pair [17,1] and lack of postorbital contribution to orbital margin [4,1] with Acctran optimization) or (2) derived features appearing late in the tristichopterid history (node 5: postorbital excluded from orbit [4,1] with Deltran optimization; node 3: denticulated field of the parasphenoid recede into the body of the parasphenoid (20,1); node 5 or 6 according to Deltran or Acctran optimizations: marginal coronoid tooth row present only on the coronoid [26,2]). *Edeopterion keithcrooki* was also presumed to be phylogenetically highly nested (Young et al., 2013) on account of characters including accessory vomers and contact between the parietal and the postorbital. According to our analysis, although the presence of accessory vomers suggests a highly nested tristichopterid, the rest of the character states support its sister-group relationship with *H. lindae*. Indeed, the presence of accessory vomers (15,1) appears late in the tristichopterid history (node 5). The most apical clade (node 2, *Ed. keithcrooki* and *H. lindae*) is characterized by an increase in the width of the skull demonstrated dermally with the parietals (22,1) and in the endoskeleton by the vomers + parasphenoid (21,0).

Recently, *L. radiatus* and *Eu. jenkinsi* have been described from the Upper Devonian Catskill Formation (Pennsylvania, U.S.A.) and the Upper Devonian of Nunavut, Canada (Downs et al., 2018; Daeschler et al., 2019), respectively. Whereas *E. jenkinsi* is included in the basal polytomy at the node 9, *L. radiatus* belongs to the highly nested tristichopterids (node 6). These species are known from limited material and consequently scored with a large number of question marks in our matrix. Thus, their precise phylogenetic positions should be regarded as tentative.

*Tinirau clackae* was previously included in the phylogenetic analysis of Swartz (2012), but this analysis used a large data set including Devonian and Carboniferous tetrapodomorphs and *T. clackae* and *Platycephalichthys* were out of the Tristichopteriidae. In Swartz's (2012) cladogram, *Platycephalichthys* was sister group to Elpistostegalia and *Tinirau* was sister group to (*Platycephalichthys* + Elpistostegalia). In our analysis, *T. clackae* forms a monophyletic group with *Eusthenopteron wenjukowi* (node 1). This clade appears in a more basal position than *P. bischoffi*, which belongs to the basal polytomy at node 8.

**Mandageriinae**—The grouping Mandageriinae was established by Young (2008), reused by Young et al. (2013) and Young et al. (2019), and includes Gondwanan tristichopterid taxa: *Mandageria fairfaxi*, *Cabonnichthys burnsi*, *Ed. keithcrooki* (referred to as the “undescribed tristichopterid from near Eden, NSW” in Young, 2008:332), and *Notorhizodon mackelveyi* (previously suggested but only recently added to the grouping in Young et al., 2019). Mandageriinae appears as polyphyletic in our analysis and is therefore not considered to be valid.

**Newly Added Characters**—Compared with previous phylogenetic studies on tristichopterids, six new characters have been added in our analysis (21–26), some of them based on observations made on *H. lindae*. Two of the new characters (21 and 22) represent unambiguous synapomorphies for the clade including *H. lindae* and *Ed. keithcrooki*. Those two characters are width/

length ratios implying a widening of the palate and of the skull roof, respectively, in clade 2. The maximum height of the maxilla at the lacrimal-jugal junction (24,1) is one of the unambiguous synapomorphies of clade 3 (*Es. wangsjoii* (*Ed. keithcrooki* + *H. lindae*)), whereas ‘a large portion (half or more) of the lacrimal rostral to the orbit’ (25,0) is one of the unambiguous synapomorphies of clade 4. Character 26 may be the synapomorphy of clade 6 or clade 5, depending on the optimization (Deltran or Acctran). Character 23 (state 1) is one of the three unambiguous synapomorphies of clade 9.

### Biogeographic History of Tristichopteriidae

The origin of the whole tristichopterid clade (node 11, Fig. 8) is most probably earlier than Givetian in age (Friedman and Brazeau, 2011) if we consider the oldest occurrences of tristichopterids, i.e., *Tristichopterus alatus*, *Notorhizodon mackelveyi*, and *Tinirau clackae* (Egerton, 1861; Young et al., 1992; Schultze and Reed, 2012; Swartz, 2012). This clade has a highly probable western European origin, which is in agreement with the Laurasian origin proposed by Ahlberg and Johanson (1997), but contradicts Young's hypothesis (2008) of a Gondwanan origin for the whole group. This western European origin is mainly due to the basal position of *Tristichopterus alatus*, which comes from this area.

Much of the early tristichopterid history took place in Euramerica (nodes 1 and 6–11). During the Late Devonian Period, tristichopterids most probably spread from Euramerica into Gondwana (node 6 to node 5). According to our results, whereas some tristichopterids remained in Euramerica during the Famennian (*Heddeleithys dalgleisiensis*, *L. radiatus*, and *L. socqueti*), clade 5 most likely differentiated into Australia and dispersal events occurred from Australia to Euramerica (to eastern North America [*H. lindae*] and to Greenland/western Europe [*Es. wangsjoii*]).

The Gondwana-Euramerica Devonian vertebrate interchange (or Great Devonian Interchange) (e.g., Janvier and Villarreal, 2000; Janvier and Clément, 2005; Young, 2008) is based on a southward dispersal of reputedly Euramerican endemics (*Holoptychius*, *Strepsodus*, and *Asterolepis*) in the Frasnian followed by a northward dispersion of Gondwanan endemics (*Groenlandaspis*, phyllolepid, rhizodontids, and megalichthyids) in the Famennian. This Frasnian–Famennian faunal interchange, in the southward direction, has recently been weakened by Olive et al. (2019). The present study supports several interchanges between Euramerica and Gondwana during the Middle–Late Devonian. Two of them correspond to Famennian migrations, in the northward direction (*E. wangsjoii* and *H. lindae*), and fit to the northward dispersions of the Great Devonian Interchange scenario. However, those results should be considered cautiously because of our still fragmentary understanding of both tristichopterid diversity and species-scale geographic distributions (most tristichopterid species are only known from a single geographic locality).

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