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Tristichopterids (Sarcopterygii, Tetrapodomorpha) from the Upper Devonian tetrapod-bearing locality of Strud (Belgium, upper Famennian), with phylogenetic and paleobiogeographic considerations

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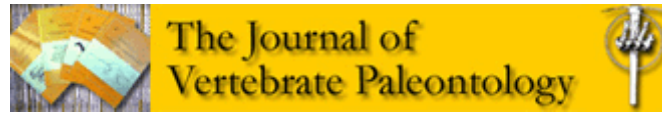
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Tristichopterids (Sarcopterygii, Tetrapodomorpha) from the Late Devonian tetrapod-bearing locality of Strud (Belgium, late Famennian), with phylogenetic and paleobiogeographic considerations

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52 RH: OLIVE ET AL.—TRISTICHOPTERIDS FROM BELGIUM
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2
3 ABSTRACT—We describe new material of the tristichopterids cf. *Langlieria socqueti* and
4
5 cf. *Eusthenodon wangsjoi* and other unassignable tetrapodomorph remains from the late
6
7 Famennian locality of Strud, Belgium. Because of recent improvements in our tristichopterid
8
9 knowledge, a new phylogenetic analysis is presented in addition to a paleobiogeographic
10
11 analysis using the Bayesian Binary MCMC statistical method. A clade formed by (*Langlieria*
12
13 *socqueti* ((*Edenopteron keithcrooki* + *Hyneria lindae*) (*Heddleithys dalglesiensis*
14
15 (*Cabonnichthys burnsi* (*Mandageria fairfaxi* + *Eusthenodon wangsjoi*)))))) represents the
16
17 most highly-nested tristichopterids and the biogeographic analysis supports a Western
18
19 European origin for it. The biogeographic analysis additionally proposes several
20
21 tristichopterid dispersal events between Euramerica and Gondwana from the Givetian to
22
23 Famennian, providing a more complex scenario than the one proposed by the Great Devonian
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25 Interchange.
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33 INTRODUCTION

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38 Tristichopteridae is a clade of elongate, aquatic sarcopterygians with an extratemporal
39
40 bone located between opercular and lateral extrascapular bones (Ahlberg and Johanson,
41
42 1997; Johanson and Ahlberg, 1997; Snitting, 2008a). Scales are devoid of cosmine, rounded
43
44 and thin with a small median boss on the internal surface. The caudal fin is trifurcate and
45
46 diamond-shaped in derived forms (Cloutier and Ahlberg, 1996).
47
48

49 Tristichopterids are known from the Middle Devonian (latest Givetian; Egerton, 1861;
50
51 Young et al., 1992; Swartz, 2012) through the Upper Devonian (Famennian; Jarvik, 1952;
52
53 Clément, 2002; Clément et al., 2009). Their body sizes ranged from 30 centimeters to several
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55 meters in length. These lobe-finned predatory vertebrates are quite common in the Devonian
56
57 vertebrate assemblages of the world with about twenty described species, but only
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3 *Eusthenodon wangsjoii* has a cosmopolitan distribution (Laurussia and Gondwana; Ahlberg et
4 al., 2001; Clément, 2002; Clément and Boisvert, 2006; Clément et al., 2009). Unassignable
5 tristichopterid remains are known from Morocco (Lehman, 1977; Lelièvre and Janvier, 1986;
6 Lelièvre et al., 1993), from Colombia (Janvier and Maisey, 2010; Olive et al., **in review**) and
7 probably from Iran (Davesne et al., 2015).

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Several studies have been done on tristichopterids from Belgium (Lohest, 1888;
Cloutier and Candilier, 1995; Clément, 2002; Clément et al., 2009; Olive et al., 2015a).
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., 2009); and unassignable tristichopterid scales from Becco, Liège
Province (Olive et al., 2015a). Tristichopterid remains have also been reported from the
locality 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 (Swartz, 2012; Schultze and
Reed, 2012; Young et al., 2013; Borgen and Nakrem, 2016; Daeschler and Downs, 2018;
Downs et al., 2018). We use our resulting cladogram as the basis for a study of the
paleobiogeographic history of Tristichopteridae.

GEOLOGICAL SETTING

During the late Famennian, 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), Vesdre Area,

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2
3 Theux Tectonic Window, Brabant Parautochton, and Haine-Sambre-Meuse Overturned
4 Thrust Sheets (HSM OTS; Fig. 1). These Variscan structures form the Namur-Dinant Basin,
5
6 which developed during Devonian and Carboniferous times (Thorez et al., 2006). Famennian
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8 outcrops from Belgium show a regressive trend from shales formed in an open marine
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10 environment (Famenne Group, early Famennian) to fluvio-lagunal siltstones, sandstones, and
11
12 dolomites (Evieux Formation, lower Famennian) (Thorez and Dreesen, 1986). Late
13
14 Famennian deposits from HSM OTS, Vesdre Area, and Theux Tectonic Window are more
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16 proximal and the fluvio-lagunal facies are generally better developed than in contemporary
17
18 deposits from the Dinant Synclinorium (Thorez et al., 2006). The strata at Strud belong to the
19
20 HSM OTS. Tristichopterid remains were found in beds A, B, D–D', and E of lithological unit
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22 7 (Fig. 1). Lithological unit 7 belongs to the late Famennian Evieux Formation. The
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24 sedimentology of this unit corresponds to the filling sequence of a channel in an alluvial plain
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26 (Denayer et al., 2016).
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35 MATERIAL AND METHODS

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40 **Preparation and Imaging**

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42 All specimens were mechanically prepared except for a few specimens that were
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44 virtually prepared by conventional X-ray tomography at the AST-RX (Accès Scientifique à la
45
46 Tomographie à Rayons X) facility of the MNHN. Scanning parameters were as follows:
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48 voltage = 85 kV, current = 260 μ A; for IRSNB P 9918, number of slices = 3000, voxel size =
49
50 0.029 mm. IRSNB P 9919 is included in three rock blocks that were scanned independently.
51
52 IRSNB P 9919a, number of slices = 1500, voxel size = 0.098 mm; IRSNB P 9919b, number
53
54 of slices = 2000, voxel size = 0.098 mm; IRSNB P 9919c, number of slices = 1800, voxel
55
56 size = 0.116 mm. IRSNB P 9918 and 9919 were virtually reconstructed with MIMICS
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3 (Materialise's Interactive Medical Image Control System) 16.0 Software (Materialise Inc.;
4
5
6 proprietary software at the MNHN) at the Atelier 3D, Centre de Recherche en Paléontologie -
7
8 Paris, MNHN.
9

10 11 12 **Phylogenetic Analysis** 13

14
15 Ahlberg and Johanson (1997) generated a phylogenetic analysis of Tristichopteridae
16
17 that has served as a starting point for subsequent analyses focusing on the clade (*e.g.*
18
19 Johanson and Ahlberg, 2001; Snitting, 2008b; Clément et al., 2009; Swartz, 2012). The
20
21 phylogenetic study developed for the present paper considers 15 species and is the first
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23 published analysis to include *Hyneria lindae* and *Edenopteron keithcrooki*. We chose to
24
25 perform a species-level analysis because we did not want to assume that the genera are
26
27 monophyletic. The analysis used 28 morphological characters (SI 1–2). Twenty-three
28
29 characters come directly or are modified from previous analyses, and five new characters
30
31 (23–28) are introduced here. In an effort to minimize qualitative assessments in character
32
33 scoring, we included only characters with well-defined states. We checked character scores
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35 against published descriptions and figures, as well as original material for *Hyneria lindae* and
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37 *Langlieria socqueti*.
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43 We used PAUP 4.0a162 (Swofford, 2002) and the branch-and-bound search algorithm
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45 to analyze the complete matrix (SI 2). All characters were ordered, except for character #26
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47 (maximum height of maxilla in external view). We chose *Gogonasus andrewsae* and
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49 *Spodichthys buetleri* for the outgroups because they are well known and phylogenetically
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51 close to tristichopterids (Long, 1985a; Long et al., 2006; Snitting, 2008b; Holland and Long,
52
53 2009). All characters were assigned equal weight and only characters 10, 26, and 28 were
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55 defined as multistate. Bremer indices and the minimal and maximal number of
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57 synapomorphies have been produced by PAUP at each node to test the node robustness.
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3 Details of the phylogenetic analysis, and notably the character state changings, are available
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5 in SI 3. Only a few character state changings have been reported on the tree in order not to
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7 overload the figure.
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10 11 12 **Biogeographic Analysis**

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15 A biogeographic analysis was performed using Bayesian Binary MCMC (BBM), in
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17 RASP 3.1 software (Yu et al., 2015). This is a statistical method that uses Bayesian inference
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19 to reconstruct the ancestral state or biogeographical origin of clades (Ronquist and
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21 Huelsenbeck, 2003). We applied BBM on the consensus tree resulting from the phylogenetic
22
23 analysis. Nine geographical areas were designated (Australia, Greenland, Canada,
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25 Pennsylvania, Nevada, Western Europe, Eastern Europe/Russia, South Africa and Antarctica)
26
27 and each taxon was assigned to the geographical area(s) where it was found (SI 4). The
28
29 geographic categories were made according to the Late Devonian paleogeography proposed
30
31 by Scotese (2014) and Ziegler (1990). For instance, Scotland, England, Belgium were all
32
33 parts of the Rhenish Basin during the Late Devonian (Ziegler, 1990) and thus were grouped
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35 together as “Western Europe”. The BBM analysis was performed over 10^6 generations with
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37 10 Markov chains, sampling every 100 generations, with the temperature set to 0.1. The first
38
39 one hundred trees were discarded as part of the burn-in period, and the Jukes-Cantor model
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41 was used, with equal among-site rate variation. The results of the biogeographic
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43 reconstructions for each node are presented in SI 5. The results of the analysis are expressed
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45 as the probability of a given clade originating from each of nine continental areas.
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52 53 **Abbreviations**

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56 **Institutional Abbreviations**—**IRSNB**, Institut royal des Sciences naturelles de
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58 Belgique, Brussels, Belgium; **MNHN**, Muséum national d’Histoire naturelle, Paris, France.
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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.d**, cleithrum postero-dorsal crest; **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; **f1.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; **l.d**, dorsal lamina of cleithrum; **l.pb**, dorsal blade post-branchial lamina of cleithrum; **l.v**, ventral lamina of cleithrum; **la.l**, lateral vertical lamina; **la.m**, mesial vertical lamina; **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**, postorbital 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; **pr.a**, anterior process; **pr.ad**, antero-dorsal process; **pop.g**, preopercular sensory groove; **ppr**, posterior process of postorbital; **r.f**, replacement pit of middle coronoid fang; **ri.it.so**, ridge dividing intertemporal and postorbital overlapping areas; **ri.ioc**, ridge housing infraorbital sensory canal; **sp.n**, spiracular notch.

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. 2)

Referred Material—IRSNB P 9912, partial left squamosal (bone has been mechanically removed to have access to the mould of the external surface), and IRSNB P 9913, right mandible.**Locality and Horizon**—Strud quarry, Namur Province, Belgium, Evieux Formation, late Famennian, Late 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. *Langlieria 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 address in the new material.

Description

Squamosal—The squamosal (IRSNB P 9912; Fig. 2A–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 squamosal and maxilla is reversed in IRSNB P 9912 relative to the condition in a partial skull of *L. socqueti* (MNHN ARD 250) from the type locality (squamosal overlaps maxilla; Clément, 2002:text-figs. 8–9). Maxilla overlap onto the squamosal is the more common condition in Tristichopteridae; the reversed condition is otherwise known only in *Eusthenodon wangsjoi* 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 supratemporal, tabular, and possibly postspiracular.

Lower Jaw—The dentary 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:text-fig. 7), there is no marginal dentition of the dentary labial to the fangs or between the fangs and the mandibular symphysis (IRSNB P 9913, Fig. 2D–F). Among tristichopterids, a marginal dentary tooth row that appears only distal to the fangs is additionally observed in *Cabonnichthys burnsi* (Johanson and Ahlberg, 1997), *Edenopteron keithcrooki* (Young et al., 2013), and *Eusthenodon wangsjoi* (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

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3 eroded mandibular groove. The overlapping area for the first submandibular can be observed
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5 on the ventral part of infradentary 1 (IRSNB P 9913, Fig. 2D–E).
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8 Only one fang of coronoid 3 is visible in IRSNB P 9913 (Fig. 2D–F). The number of
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10 fang pairs on coronoid 3 is impossible to determine in this specimen and the condition is
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12 unknown in *L. socqueti*. Among tristichopterids, only *Spodichthys buetleri* (Snitting, 2008b),
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14 *Tristichopterus alatus* (Snitting, 2009), and *E. keithcrooki* (Young et al., 2013) are reported
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16 with one fang pair, rather than two, on coronoid 3. The coronoid fangs of IRSNB P 9913
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18 exhibit cutting-edges and striations at the base that may or may not reach to the apex of the
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20 tooth.
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24 **Dermatocranial Ornament**—The dermatocranial ornament of IRSNB P 9912 and
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26 IRSNB P 9913 is very fine. IRSNB P 9912 (squamosal) exhibits subparallel ridges in the
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28 rostrrodorsal part of the bone and anastomosing ridges elsewhere. On IRSNB P 9913 (dentary
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30 + infradentaries), the ornament is mainly made of smooth anastomosed ridges, which are
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32 more strongly pronounced at the distal end of the dentary.
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38 cf. *EUSTHENODON* Jarvik, 1952
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42 **Type Species**—*Eusthenodon wangsjoii* Jarvik, 1952.
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47 cf. *EUSTHENODON WANGSJOI* Jarvik, 1952
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49 (Figs 3–4, SI 6–7)
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54 **Referred Material**—IRSNB P 9910, partial left parietal; IRSNB P 9914, left
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56 supratemporal, part and counterpart; IRSNB P 9915, partial left postorbital; IRSNB P 9916,
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3 left preopercular; IRSNB P 9917, left opercular; IRSNB P 9918, right dentary; IRSNB P
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5 9919, partial right mandible.
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8 **Locality and Horizon**— Strud quarry, Namur Province, Belgium, Evieux Formation,
9
10 late Famennian, Late Devonian.

11
12 **Remarks**—These specimens are referred to cf. *Eusthenodon wangsjoii* on account of
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14 dermal ornament and size category. In addition, IRSNB P 9915 (postorbital) shares general
15
16 shape characteristics with the *E. wangsjoii* holotype (P. 1476) in addition to a well-developed
17
18 rostradorsal process (Jarvik, 1952:pl. 9). IRSNB P 9917 (preopercular) has a wide
19
20 rostroventral process similar to that observed in the *E. wangsjoii* holotype (Jarvik, 1952:pl.
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22 10). General shape characteristics are shared between IRSNB P 9914 (supratemporal) and
23
24 IRSNB P 9918 (opercular) and the *E. wangsjoii* holotype (Jarvik, 1952:pl. 9). IRSNB P 9919
25
26 (mandible) shares with the *E. wangsjoii* holotype (Jarvik, 1952:pl. 10) a lack of fusion among
27
28 the dermatocranial mandibular bones.
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35 **Description**

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37 **Parietal**—IRSNB P 9910 (Fig. 3A–B) is an isolated partial parietal that preserves
38
39 much of the caudal margin and the medial margin. The dermal surface of the parietal exhibits
40
41 a short area of supratemporal overlap along the caudolateral margin. The posterior oblique
42
43 pitline groove is observed lateral to the pineal region. The shape of the parietal suggests a
44
45 kite-shaped pineal series, contrary to the tear-drop shaped condition in the *Eusthenodon*
46
47 *wangsjoii* holotype (P. 1476; Jarvik, 1952:pl. 9) and in Clément's (2002) emended diagnosis
48
49 of the species. In addition, it appears as though the pineal series either reaches or nearly
50
51 reaches the caudal margin of the parietal shield. Several specimens of *E. wangsjoii* (including
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53 the holotype, P. 1476; Jarvik, 1952:pl. 9) show a more rostrally positioned pineal series. High
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3 variability of pineal positioning in *E. wangsjoii* has previously been recognized by Jarvik
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5 (1985).
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7
8 **Supratemporal**—IRSNB P 9914 (Fig. 3C–F) is widest along its caudal margin and
9
10 the spiracular notch is strongly hook-shaped. This shape is quite different from what is
11
12 observed in the *Eusthenodon wangsjoii* holotype (P. 1476; Jarvik, 1952) and more closely
13
14 resembles the condition observed in *Eusthenopteron foordi* (e.g., Jarvik, 1944a). Areas
15
16 overlapped by the intertemporal and postorbital are observed on the dermal surface of the
17
18 supratemporal (Fig. 3C), in the rostromedial corner. A strong ridge divides the two overlap
19
20 areas (Fig. 3E) as in *Langlieria socqueti* (Clément, 2002:fig. 6B). On the visceral
21
22 surface, a smooth depression is visible anteriorly. This depression may have received the
23
24 palatoquadrate paratemporal process (as proposed by Clément, 2002, for *E. wangsjoii*). The
25
26 ridge housing the infraorbital canal is present around this depression. A possible articulation
27
28 area with the hyomandibula is located in the caudomedial corner (Fig. 3F).
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33 **Postorbital**—IRSNB P 9915 (Fig. 3G–H) is an isolated partial postorbital with an
34
35 extended shared area for the overlap of both intertemporal and posterior supraorbital bones.
36
37 These overlap areas are not observable in the *Eusthenodon wangsjoii* type material.
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39

40 **Preopercular**—IRSNB P 9916 (Fig. 3I–J) is a partial left preopercular that preserves
41
42 an area for squamosal overlap that appears short but may be incomplete.
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44

45 **Opercular**—IRSNB P 9917 (Fig. 3K–L) is an opercular with a high height/length
46
47 ratio (1.5). Jarvik (1952) described the opercular of *Eusthenodon wangsjoii* as higher than
48
49 long and figures a single specimen (P. 1481, Jarvik, 1952:pl. 12:2) with a ratio that is not as
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51 high (=1.24) as that in IRSNB P 9917. The ventral margin of IRSNB P 9917 is rounded as in
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53 *Eusthenopteron foordi* (e.g., Jarvik, 1944a) and is notably unlike the condition in
54
55 *Cabonnichthys burnsi* (Ahlberg and Johanson, 1997:fig. 3), where the margin is indented by
56
57 the subopercular. The dorsal margin of IRSNB P 9917 shows a well-developed and large
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3 overlap area divided in two parts by a ridge. The larger rostral part was probably for the
4
5 postspiracular bone and the smaller caudal part for the lateral extrascapular. In *E. wangsjoii*,
6
7 only the overlap area for the postspiracular has been previously reported (by Jarvik, 1952:pl.
8
9 12:2). However, Jarvik (1952:64) expresses doubt over whether the area was overlapped by
10
11 the postspiracular or the lateral extrascapular. The rostral margin of IRSNB P 9917 displays a
12
13 very narrow overlap area for the preopercular.
14
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17 **Lower Jaw**—IRSNB P 9918 (Fig. 4A–B) exhibits a dentary fang pair and no
18
19 marginal teeth are observed from the fang pair to the symphysis. Within Tristichopteridae,
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21 this condition is shared among *Cabonnichthys burnsi* (Johanson and Ahlberg, 1997),
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23 *Edenopteron keithcrooki* (Young et al., 2013), and *Eusthenodon wangsjoii* (Jarvik, 1952;
24
25 Johanson, 2004). IRSNB P 9919 (Fig. 4D–F) includes all three coronoids. Coronoid 3 is
26
27 much longer than coronoids 1 or 2. Among tristichopterids, only *Spodichthys buetleri*
28
29 (Snitting, 2009) and *Tristichopterus alatus* (Snitting, 2009) have been reported with a third
30
31 coronoid of a length subequal to coronoids 1 and 2. The fangs of coronoids 1 and 2 have
32
33 sharp carinae along mesial and distal margins. The fangs of both pairs on coronoid 3 are
34
35 much smaller than those of coronoids 1 or 2. No striations are visible on the coronoid fangs
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37 of IRSNB P 9919. A marginal tooth row is not visible on any of the three coronoids of
38
39 IRSNB P 9919. This may be a result of preservation; no other tristichopterid is without
40
41 marginal coronoid dentition. Among tristichopterids, the most reduced condition previously
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43 recognized (marginal teeth on third coronoid only) is observed in *E. wangsjoii* (Jarvik, 1952),
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45 *Hynertia lindae* (Daeschler and Downs, 2018), and *M. fairfaxi* (Johanson and Ahlberg, 1997).
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51 **Dermatocranial Ornament**—As described in Clément's (2002) emended diagnosis
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53 for *Eusthenodon wangsjoii*, the dermatocranial ornament of these Strud specimens consists of
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55 ridges forming distinct networks and independent tubercles are rare.
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DESCRIPTION OF OTHER TRISTICHOPTERID MATERIAL FROM STRUD

Unless otherwise noted, the specimens reported below are referred to cf.

Tristichopteridae sp. indet. according to shapes, sizes, and dermal ornaments that compare more favourably to Strud's tristichopterids than to the other vertebrates at the locality (acanthodians, actinopterygians, antiarchs, arthrodiros, phyllolepidids, porolepiforms, rhizodonts, osteolepidids, dipnoans, tetrapods; Lohest, 1888; Leriche, 1931; Clément et al., 2004; Clément and Boisvert; 2006; Olive, 2015; Olive et al., 2015b, 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. 5A) is a right preopercular with a deep dorsal–ventral sensory groove in its caudal half. Its ornamentation comprises small tubercles and ridges.

IRSNB P 9921–9923 (Fig. 5B–D) are isolated subopercular bones. The rostral process of IRSNB P 9921 is especially long and rod-like (Fig. 5B). IRSNB P 9923 is much smaller than the other two and has a more rounded shape with a short, stout rostral process (Fig. 5D).

IRSNB P 9911 (Fig. 5E–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. 5F). The rostral end of the specimen exhibits a pronounced autopalatine process and a ventral process of the

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3 entopterygoid with a short triangular groove between them that tapers caudally. A prominent
4 ascending process is partially observed at the dorsal preservational limit. A row of large and
5 pointed denticles appear along the ventral margin of the entopterygoid's rostral end. The
6
7 ventral margin of the palatoquadrate is relatively straight and does not exhibit the wide lateral
8
9 flange that surrounds the caudal end of the ectopterygoid in *Eusthenodon wangsjoi* (Jarvik,
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11 1952:pl. 16:2).

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IRSNB P 9924–9927 are isolated cleithra. The dorsal lamina ornament of IRSNB P
9924 (Fig. 6A–B) is a network of generally parallel fine anastomosed crests; that of IRSNB P
9926 and IRSNB P 9927 (Fig. 6E–F) is coarse tubercles and small ridges similar to cleithrum
ornament of *Platycephalichthys bischoffi* (Vorobyeva, 1959, 1962) and *Langlieria socqueti*
(Clément, 2002; Clément et al., 2009). The dorsal lamina of IRSNB P 9925 (Fig. 6D) is
generally smooth, perhaps due to weathering. In IRSNB P 9925, a long crest follows the
caudal margin of the dorsal lamina's visceral surface. (Fig. 6D).

IRSNB P 9928 and 9929 (Fig. 6G–H) are isolated fangs with ridges along their base
and sharp carinae along mesial and distal edges.

IRSNB P 9930–9933 (Fig. 6I–L) are isolated scales. Each shows the visceral boss that
allows an assignment to Tristichopteridae sp. indet. Several (IRSNB P 9930–9931, IRSNB P
9933) show radiating grooves on the free margin.

RESULTS

Phylogenetic Analysis

The phylogenetic analysis of the complete data matrix yielded three most
parsimonious trees with a score of 62 (CI = 0.5; RI = 0.617; RCI = 0.309). Figure 7 presents
the 50% majority-rule consensus tree that was generated from the data. Bremer indices are all

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3 equal to 1 except the clade (*Cabonnichthys burnsi* (*Mandageria fairfaxi* + *Eusthenodon*
4 *wangsjoii*)), which has a Bremer index of 2.
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8 Usually considered as a tristichopterid, *Tristichopterus alatus* has an unresolved basal
9 position in our phylogenetic analysis. It belongs to the basal polytomy with the two outgroups
10 and the rest of the tristichopterids (node 11).
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13
14 Node 11 is characterized by five synapomorphies: presence of epichordal radials in
15 the caudal fin (character 1, state 1), a pineal foramen well posterior to orbits (9,1), two fang
16 positions on posterior coronoid (12,1), a posterior coronoid much longer than middle
17 coronoid (13,1) and a dentary fang pair (18,1).
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21 Node 10 is characterized by a symmetrical caudal fin (2,1), a posterior process of the
22 posterior supraorbital much longer than its orbital margin (7,1), two fang positions on
23 ectopterygoid (11,1), less than half of the lacrimal rostral to orbit (27,1) and the presence of
24 an extratemporal in a postspiracular position (21,1).
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27
28 *Eusthenopteron* (node 1) is characterized by the lack of epichordal radials in the
29 caudal fin (1,0), the absence of a dentary fang pair (18,0) and a straight or slightly concave
30 lateral margin of the vomer's caudal process (19,1).
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34 In our analysis, and contrary to Borgen and Nakrem (2016), the ancestral character
35 state for the premaxillary dentition (character 10) is not homodonty (morphotype A, state 0),
36 but instead a gradual tooth size increase with proximity to the symphysis (state 1).
37 Homodonty is a derived character, which occurred independently in *Spodichthys buetleri*,
38 *Eusthenopteron wenjukowi*, and *Platycephalichthys bischoffi*. A single, greatly enlarged
39 premaxillary fang (state 2; morphotypes C and D of Borgen and Nakrem, 2016) supports the
40 clade of Famennian tristichopterids (node 7). It also appears independently in *Tinirau*
41 *clackae*. The Famennian tristichopterid clade (node 7) is also supported by the lack of dentary
42 marginal teeth near the symphysis (14,1).
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3 In this analysis, the best supported clades are (*Hyneria lindae* + *Edenopteron*
4 *keithcrooki*) (minimal and maximal number of synapomorphies of five and six) and
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8 ((*Eusthenodon wangsjoii* + *Mandageria fairfaxi*) *Cabonnichthys burnsi*) (Bremer index of 2).
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10 The first is characterized by the absence of contact between the posterior supraorbital and the
11
12 intertemporal (5,1), an apical fossa divided in two (20,1), a flat to concave denticulated field
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14 of the parasphenoid (22,0), a 0.5 or greater width/length ratio of vomers + parasphenoid
15
16 (23,0), a 0.5 or greater width/length ratio of parietals (24,1), and a maxilla overlap onto
17
18 squamosal (25,0). *Edenopteron keithcrooki* has only one fang position on its posterior
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20 coronoids (12,0) and this reversal makes it unique within the Famennian tristichopterid clade
21
22 (node 7).
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26 The second of the best supported clades, ((*Eusthenodon wangsjoii* + *Mandageria*
27 *fairfaxi*) *Cabonnichthys burnsi*), is characterized by the absence of a vertical blade-like
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29 lamina lateral to the fangs of coronoid 1 (15,1), a marginal coronoid tooth row on coronoid 3
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31 only (28,2), the presence of accessory vomers (16,1) and a maxilla of equal height along its
32
33 entire length (26,2). *E. wangsjoii* and *M. fairfaxi* share the following combination of
34
35 characters: jugal excluded from orbital margin (3,1), an absence of contact between posterior
36
37 supraorbital and intertemporal (5,1), a contact between posterior supraorbital and lacrimal
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39 (6,1), absence of a marginal tooth row mesial to the dermatopalatine fang (17,1) and half or
40
41 more of the lacrimal appears rostral to the orbit (27,0). The relationships among *E. wangsjoii*,
42
43 *M. fairfaxi* and *C. burnsi* agree with the results of Ahlberg and Johanson (1997, 1998, 2001)
44
45 and place *Cabonnichthys* as the sister taxon of (*Eusthenodon* + *Mandageria*).
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54 **Biogeographic Analysis**

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56 Clade 7 includes the most derived tristichopterids: *Langlieria socqueti*, *Edenopteron*
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58 *keithcrooki*, *Hyneria lindae*, *Heddeleithys dalglesiensis*, *Cabonnichthys burnsi*,
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3 *Mandageria fairfaxi* and *Eusthenodon wangsjoii*. This node is reconstructed with a Western
4 Europe origin (~84% probability).
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8 Clade 4 gathers taxa (*Cabonnichthys burnsi*, *Mandageria fairfaxi* and *Eusthenodon*
9 *wangsjoii*) with an Australian origin (~81% probability) and clade 2 groups taxa
10 (*Edenopteron keithcrooki* and *Hynertia lindae*) with a possible Australian origin (~67%).
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14 The major conflict in the biogeographic reconstruction occurs at the root node 12
15 where the Australian origin is supported at 30%, the Greenland origin at 28%, the Western
16 Europe origin at 22% and the Nevada origin at 7%. This is explained by the basal polytomy
17 and the choice of the outgroups, which are themselves of Australian (*Gogonasus andrewsae*)
18 and Greenland (*Spodichthys buetleri*) origins.
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22 The basal position of *Tinirau clackae* and *Notorhizodon mackelveyi* suggest a
23 Western North America (Nevada) origin for the clade 11 (~62% probability) and an Antarctic
24 origin for clade 10 (~63% probability).
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27 28 29 30 31 32 33 34 35 DISCUSSION

36 37 38 39 40 **Phylogenetic Analysis**

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42 As mentioned by Schultze and Reed (2012), interrelationships of tristichopterids have
43 been very stable over the years and have changed only by addition of new taxa. This is the
44 case in the present analysis. Most recent phylogenetic analyses of tristichopterids support a
45 highly nested clade of tristichopterids including variably *Cabonnichthys*, *Eusthenodon*,
46 *Mandageria*, (Ahlberg and Johanson, 1997, 1998; Johanson and Ahlberg, 2001; Zhu and
47 Ahlberg, 2004; Snitting, 2008b; Clément et al., 2009; Swartz, 2012) and *Langlieria* (Clément
48 et al., 2009). The present analysis gathers the same taxa (node 7) and additionally includes
49 *Hynertia lindae* and *Edenopteron keithcrooki*, both included for the first time in a published
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3 phylogenetic analysis. The clade of Famennian tristichopterids that originates at node 7
4 additionally includes *Heddleithys dalglesiensis*.

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8 **Position of *Spodichthys***—*Spodichthys* is basal to all tristichopterids in all
9
10 phylogenetic analyses where it is included (Snitting, 2008a, 2008b; Clément et al., 2009). It
11 displays a number of plesiomorphic characters such as the absence of contact between the
12 posterior supraorbital and the intertemporal (5,1), the pineal foramen located at the level with
13 or anterior to the posterior margin of the orbit (9,0), only one fang position on the
14 ectopterygoid and third coronoid (11,0 and 12,0), a third coronoid similar in length to the
15 middle coronoid (13,0), the presence of a vertical lamina lateral to the coronoid fang on the
16 anterior coronoid (15,0), the absence of a dentary fang pair (18,0) and a width/length ratio of
17 vomers + parasphenoid equal to or more than 0.5 (23,0). In our analysis, *Spodichthys buetleri*
18 appears in a basal polytomy together with *Gogonasus andrewsae*, *Tristichopterus alatus* and
19 a clade that contains all other Tristichopteridae. The phylogenetic position of *S. buetleri*
20 remains an open question because more than half of the characters are missing data (19 of
21 28). It is considered to be the sister group of Tristichopteridae by Snitting (2008b) because it
22 cannot be demonstrated that its extratemporal reaches into the postspiracular area, a feature
23 that diagnoses Tristichopteridae.

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42 **Monophyly of Tristichopteridae**—Tristichopterid monophyly has been established
43 in several studies (Long, 1985b; Ahlberg and Johanson, 1997, 1998; Johanson and Ahlberg,
44 2001; Zhu and Ahlberg, 2004; Snitting, 2008a, 2008b; Clément et al., 2009). In the present
45 analysis, because of the low resolution at the base of the tree, this monophyly is not
46 specifically supported. The presence of an extratemporal in a postspiracular position (21,1), a
47 feature used to diagnose members of Tristichopteridae, is here regarded as a synapomorphy
48 of clade 10 only. It is absent in *Tinirau clackae* (the ‘postspiracular’ is in a rostral position)
49 and its presence in *Tristichopterus alatus* is regarded as a convergence.

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3 **Newly Added Taxa**—*Edenopteron keithcrooki* and *Hyneria lindae* are included in a
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5 phylogenetic analysis for the first time and these appear as sister species to one another (node
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7 2). Node 2 is supported by six synapomorphies (see Results) including the division of the
8
9 apical fossa into two parts, a condition that is unique within Tristichopteridae.

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12 The position of *H. lindae* within tristichopterids appears as less derived than
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14 previously thought by several authors (Daeschler and Shubin, 2007; Clément et al., 2009;
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16 Daeschler and Downs, 2018). In a previous publication by two of us (Daeschler and Downs,
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18 2018), a highly nested phylogenetic position for *H. lindae* was proposed due to a suite of
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20 characters that includes contact between parietal and postorbital, a postorbital that does not
21
22 contribute to the orbital margin, a wide and concave denticulated plate of the parasphenoid, a
23
24 dentary fang pair, and a lack of marginal dentition on all but the third coronoid. Except for
25
26 the last character (28,2), the new phylogenetic analysis supports all of these as either derived
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28 features appearing quite early in the history of tristichopterids (dentary fang pair (18,1) and
29
30 lack of postorbital contribution to orbital margin (4,1)) or plesiomorphic for the group (wide
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32 and concave denticulated plate of the parasphenoid, 22,0).

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35 *Edenopteron keithcrooki* was also presumed to be phylogenetically highly nested
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37 (Young et al., 2013) on account of characters including accessory vomers and contact
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39 between parietal and postorbital. According to our analysis, while the presence of accessory
40
41 vomers suggests a derived tristichopterid, the rest of the character states support its sister
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43 group relationship with *H. lindae*.

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46 *Tinirau clackae* was previously included in the phylogenetic analysis of Swartz
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48 (2012) but this analysis used a large dataset including Devonian and Carboniferous
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50 tetrapodomorphs. As noticed by Young et al. (2013), the character list diluted characters
51
52 relevant to tristichopterids and pushed *T. clackae* and *Platycephalichthys* out of
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54 Tristichopteridae. In Swartz's (2012) cladogram, *Platycephalichthys* was sister group to
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3 Elpistostegalia and *Tinirau* was sister group to (*Platycephalichthys* + Elpistostegalia). In our
4 analysis, the only species in these two groups occupy basal position within Tristichopteridae.
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8 **Mandageriidae**—The subfamily Mandageriidae was established by Young (2008)
9 and includes Gondwana tristichopterid taxa: *Mandageria fairfaxi*, *Cabonnichthys burnsi*,
10 possibly *Notorhizodon mackelveyi* and *Edenopteron keithcrooki* (referred to as the
11 “undescribed tristichopterid from near Eden, NSW” in Young, 2008). According to Young
12 (2008), who did not perform a phylogenetic analysis to support his assertion, features
13 justifying the erection of this subfamily were a shared scale morphology and the presence of
14 accessory vomers. This pairing is counter to the relationships presented in Ahlberg and
15 Johanson’s (1997) phylogenetic analysis, wherein *M. fairfaxi* is the sister group of
16 *Eusthenodon wangsjoii*, not *Cabonnichthys burnsi*. One of Young’s (2008) arguments against
17 the pairing of *M. fairfaxi* and *E. wangsjoii* was the weakness of the only synapomorphy that
18 supported it. According to Young (2008), absence of contact between intertemporal and
19 posterior supraorbital is impossible to assess in *M. fairfaxi*.
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35 In our phylogenetic analysis, we respond to the issues raised by Young (2008). The
36 “accessory vomers” character has been added (ch.16; as it was already done by Clément et
37 al., 2009). We scored character 5 (contact between posterior supraorbital and intertemporal)
38 in the same way as Ahlberg and Johanson (1997) for *Mandageria fairfaxi* and *Cabonnichthys*
39 *burnsi* since we do not have access to the type material, but whereas the absence of contact
40 was only a shared character by *E. wangsjoii* and *M. fairfaxi*, in our matrix, it is additionally
41 shared by *E. keithcrooki* and *H. lindae*. We also add characters and key species that should
42 help to address the validity of the subfamily Mandageriidae (*i.e.*, *N. mackelveyi* and *E.*
43 *keithcrooki*).
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56 The relationships supported by our analysis are those originally presented by Ahlberg
57 and Johanson (1997, 1998) and also Clément et al. (2009): (*C. burnsi* (*M. fairfaxi* + *E.*
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3 *wangsjoi*). The clade (*M. fairfaxi* + *E. wangsjoi*) is supported by five synapomorphies and
4 displays a minimal and maximal numbers of synapomorphies of four and six. Mandageriidae
5 appears as paraphyletic here and is therefore not considered to be valid.
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10 **Newly Added Characters**—Compared to previous phylogenetic studies on
11 tristichopterids, six new characters have been added in our analysis, some of them based on
12 observations made on *Hynertia lindae*. Half of the new characters (23, 24, and 25) represent
13 unexpected synapomorphies for the clade including *Hynertia lindae* and *Edenopteron*
14 *keithcrooki*. Characters 23 and 24 are width/length ratios implying a widening of the palate
15 and of the skull roof, respectively, in clade 17. A marginal coronoid tooth row that is only
16 present on coronoid 3 represents a new synapomorphy for the highly nested group of
17 tristichopterids: (*Cabonnichthys burnsi* (*Mandageria fairfaxi* + *Eusthenodon wangsjoi*)).
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31 **Biogeographic History of Tristichopteridae**

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33 There is a perfect congruence between the phylogenetic and stratigraphic data (Fig.
34 7). The origin of the whole group would be, at least, Givetian in age if we consider the oldest
35 occurrence of tristichopterids, *i.e.* *Tristichopterus alatus*, *Notorhizodon mackelveyi*, and
36 *Tinirau clackae* (Egerton, 1861; Young et al., 1992; Swartz, 2012; Schultze and Reed, 2012).
37 More derived tristichopterids (*Eusthenopteron foordi*, *Eusthenopteron wenjukowi* and
38 *Platycephalichthys bischoffi*) are Frasnian in age and the most derived clade (from node 7) is
39 Famennian in age.
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49 Concerning the origin of the Tristichopteridae whole group (except *Tristichopterus*
50 *alatus*, which is in the basal polytomy), node 11 is unambiguously reconstructed with a
51 Western North American origin. This Laurussian origin agrees with Ahlberg and Johanson
52 (1997) and disagrees with Young (2008) who argued for a Gondwanan origin of the whole
53 group. This Western North American origin is mainly due to the basal position of *Tinirau*
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3 *clackae*, which comes from this area. This is also due to the fact that *Tristichopterus alatus*
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5 ends up in the basal polytomy. If it instead occupied a resolved and most basal position
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7 within Tristichopteridae (as in Clément et al., 2009; Ahlberg and Johanson, 1997), the origin
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9 of the entire group would be Western European.
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12 The origin of node 10 is reconstructed with a Gondwanan origin (Antarctica). This is
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14 explained by the basal position of *Notorhizodon mackelveyi*. According to these results, and
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16 as previously proposed by Johanson and Ahlberg (2001), tristichopterids would have already
17
18 achieved a worldwide distribution as early as the Givetian. Our biogeographic analysis also
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20 proposes dispersal from Gondwana (Antarctica) to Laurussia (Eastern Europe) during the
21
22 Givetian–Frasnian (node 10 to 9).
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26 During the Late Devonian Period, our results support an expansion of tristichopterids
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28 from Eastern Europe into Western Europe (node 8 to node 7). Much of tristichopterid history
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30 took place in Laurussia (nodes 1 and 5–9), first in Eastern Europe (nodes 9, 8, and 1) and
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32 then in Western Europe (nodes 5–7), with the introgression of one taxon (*Eusthenopteron*
33
34 *foordi*) into Western Laurussia (Canada).
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38 According to these results, while some tristichopterids remained in Europe during the
39
40 Famennian (*Heddleithys dalgleisiensis* and *Langlieria socqueti*), dispersal events occurred
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42 from Western Europe to Australia (one from node 6 to 2 and another from node 5 to 4) and at
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44 least once from Australia to Eastern North America (*H. lindae*). *Eusthenodon wangsjoii*, with
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46 its remarkable distribution, expanded out of Australia, in the Famennian, to reach Greenland,
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48 Europe, and Antarctica. These hypothesized Famennian tristichopterid dispersal events are
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50 difficult to reconcile with modern paleogeographic reconstructions. We might expect such
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52 discrepancies to result from our still fragmentary understanding of both tristichopterid
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54 diversity and species–scale geographic distributions (most tristichopterid species are only
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56 known from a single geographic locality).
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3 The Gondwana-Euramerica Devonian vertebrate interchange (or Great Devonian
4 Interchange) (e.g., Janvier and Villarroel, 2000; Janvier and Clément, 2005; Young, 2008) is
5 a proposed southward dispersion of reputedly Euramerican endemics (*Holoptychius*,
6 *Strepsodus* and *Asterolepis*) in the Frasnian followed by a northward dispersion of
7 Gondwanan endemics (*Groenlandaspis*, phyllolepid, rhizodontids and megalichthyids) in
8 the Famennian. This Frasnian–Famennian faunal interchange, at least in the southward
9 direction, has recently been weakened by Olive et al. (in review). The present study supports
10 several interchanges between Euramerica and Gondwana during the Middle–Late Devonian.
11 The first is a southward migration during the Givetian (node 11 to 10) and could correspond
12 to a time-extended southward migration of the Great Devonian Interchange. The second is a
13 Givetian–Frasnian northward migration (node 10 to 9) that contradicts the Interchange, and
14 then there are several Famennian migrations, mainly in the southward direction. Although
15 our results are preliminary, they lend some support to tristichopterid distributional patterns
16 that are more complex than the proposed Great Devonian Interchange.

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Figure Captions

FIGURE 1. Geographical and geological localizations of Belgian tristichopterid localities including Strud (Namur Province). **A**, Geographic localities; **B**, Geological map of Southern Belgium, modified from Denayer et al. (2016), redrawn from Béthune (1954); **C**, schematic block diagram of the Strud channel with the location of tristichopterid remains, modified from Denayer et al (2016). [planned for page width]

FIGURE 2. cf. *Langlieria socqueti*, Strud, Belgium, late Famennian. **A**, left squamosal, internal view, IRSNB P 9912, photograph; **B**, left squamosal, imprint of the external surface (bone removed), IRSNB P 9912, photograph; **C**, left squamosal, external view, IRSNB P 9912, interpretative drawing; **D**, right mandible, external view, IRSNB P 9913, photograph; **E**, right mandible, external view, IRSNB P 9913, interpretative drawing; **F**, right mandible, external view, IRSNB P 9913, close-up photograph on the symphysis. Scale bars equal 1 cm. [planned for page width]

FIGURE 3. cf. *Eusthenodon wangsjoii*, Strud, Belgium, Upper Famennian. **A**, incomplete left parietal, external view, IRSNB P 9910, photograph; **B**, incomplete left parietal, external view, IRSNB P 9910, interpretative drawing; **C–D**, left supratemporal, external and visceral views, IRSNB P 9914, photographs; **E–F**, left supratemporal, external and visceral views, IRSNB P 9914, interpretative drawings; **G**, left postorbital, external view, IRSNB P 9915, photograph; **H**, left postorbital, external view, IRSNB P 9915, interpretative drawing; **I–J**, left preopercular, external and visceral views, IRSNB P 9916, photographs; **K**, left opercular, external view, IRSNB P 9917, photograph; **L**, left opercular, external view, IRSNB P 9917,

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3 interpretative drawing. Black arrow points anteriorly. Scale bars: **A–H** equal 1 cm, **I–L** equal
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5 2 cm. [planned for page width]
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10 FIGURE 4. cf. *Eusthenodon wangsjoii*, Strud, Belgium, late Famennian. **A**, right dentary,
11 external view, IRSNB P 9918, 3D reconstruction; **B**, right dentary, visceral view, IRSNB P
12 9918, 3D reconstruction; **C**, right mandible, external view, IRSNB P 9919, 3D
13 reconstruction; **D**, right mandible, visceral view, IRSNB P 9919, 3D reconstruction; **E**,
14 coronoids, external view, IRSNB P 9919, 3D reconstruction; **F**, coronoids, apical view,
15 IRSNB P 9919, 3D reconstruction. Left white arrow indicates putative suture between the
16 infradentaries 3 and 4, right white arrow indicates pit line of infradentary 2. Black arrow
17 points anteriorly. Scale bars: **A–B**, **E–F** equal 1 cm, **C–D** equal 2 cm. [planned for page
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33 FIGURE 5. cf. Tristichopteridae indet., Strud, Belgium, Upper Famennian. **A**, right
34 preopercular, external view, IRSNB P 9920, photograph; **B**, left subopercular, visceral view,
35 IRSNB P 9921, photograph; **C**, left subopercular, visceral view, IRSNB P 9922, photograph;
36 **D**, left subopercular, visceral view, IRSNB P 9923, photograph; **E**, right palatoquadrate,
37 visceral view, IRSNB P 9911, photograph; **F**, right palatoquadrate, visceral view, IRSNB P
38 9911, interpretative drawing. Black arrow points anteriorly. Scale bars equal 1 cm. [planned
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51 FIGURE 6. cf. Tristichopteridae indet., Strud, Belgium, Upper Famennian. **A**, right
52 cleithrum, visceral view, IRSNB P 9924, photograph; **B**, right cleithrum, imprint of the
53 external view (bone removed), IRSNB P 9924, photograph; **C–D**, right cleithrum, external
54 and visceral views, IRSNB P 9925, photographs; **E**, incomplete right cleithrum, visceral
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3 view, IRSNB P 9926, photograph; **F**, incomplete right cleithrum, visceral view, IRSNB P
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5 9927, photograph; **G**, isolated fang, labial or lingual view, IRSNB P 9928, photograph; **H**,
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7 isolated fang, labial or lingual view, IRSNB P 9929, photograph; **I**, isolated scale, visceral
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9 view, IRSNB P 9930, photograph; **J**, isolated scale, visceral view, IRSNB P 9931,
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11 photograph; **K**, isolated scale, visceral view, IRSNB P 9932, photograph; **L**, isolated scale,
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13 visceral view, IRSNB P 9933, photograph. Scale bars equal 1 cm. [planned for page width]
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FIGURE 7. Strict consensus tree showing phylogenetic relationships of the Tristichopteridae, with maximum parsimony biogeographic reconstruction result using 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. The numbers on the top of each pie chart correspond to the Bremer index (in italics) and to the minimal and maximal number of synapomorphies at each node (in bold). Some character state changings have been reported on the branches. GIV for Givetian, FRAS for Frasnian and FAM for Famennian. [planned for page width]

SUPPLEMENTAL INFORMATION 1. List of characters considered in the phylogenetic analysis.

SUPPLEMENTAL INFORMATION 2. Matrix of characters considered in the phylogenetic analysis.

SUPPLEMENTAL INFORMATION 3. Details of the phylogenetic analysis.

SUPPLEMENTAL INFORMATION 4. Taxon geographical distribution.

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5 SUPPLEMENTAL INFORMATION 5. Results of the maximum parsimony biogeographic
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8 reconstructions using Bayesian Binary MCMC analysis.
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12 SUPPLEMENTARY INFORMATION 6: 3D PDF of a right dentary of *Eusthenodon*
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14 *wangsjoii*. Strud, Belgium, late Famennian. IRSNB P 9918. Click to activate in the PDF
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17 version.
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21 SUPPLEMENTARY INFORMATION 7: 3D PDF of a right mandible of *Eusthenodon*
22
23 *wangsjoii*. Strud, Belgium, late Famennian. IRSNB P 9919. Click to activate in the PDF
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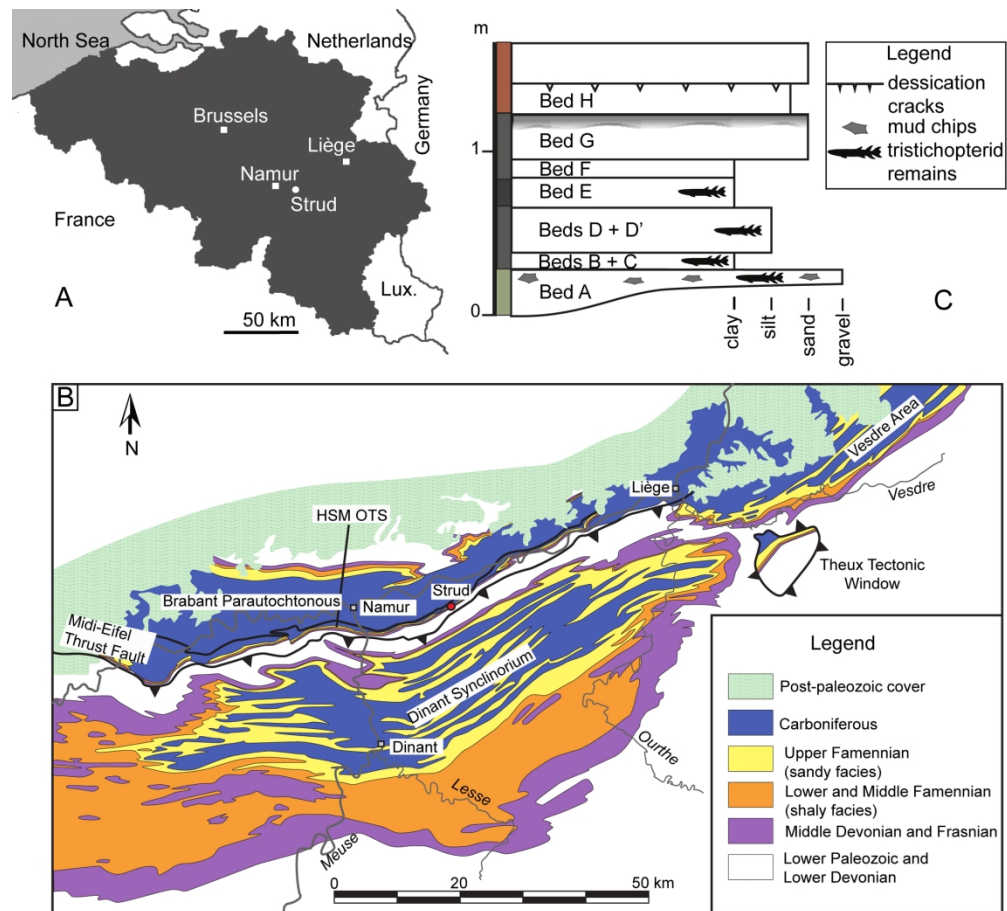


FIGURE 1. Geographical and geological localizations of Belgian tristichopterid localities including Strud (Namur Province). A, Geographic localities; B, Geological map of Southern Belgium, modified from Denayer et al. (2016), redrawn from Béthune (1954); C, schematic block diagram of the Strud channel with the location of tristichopterid remains, modified from Denayer et al (2016). [planned for page width]

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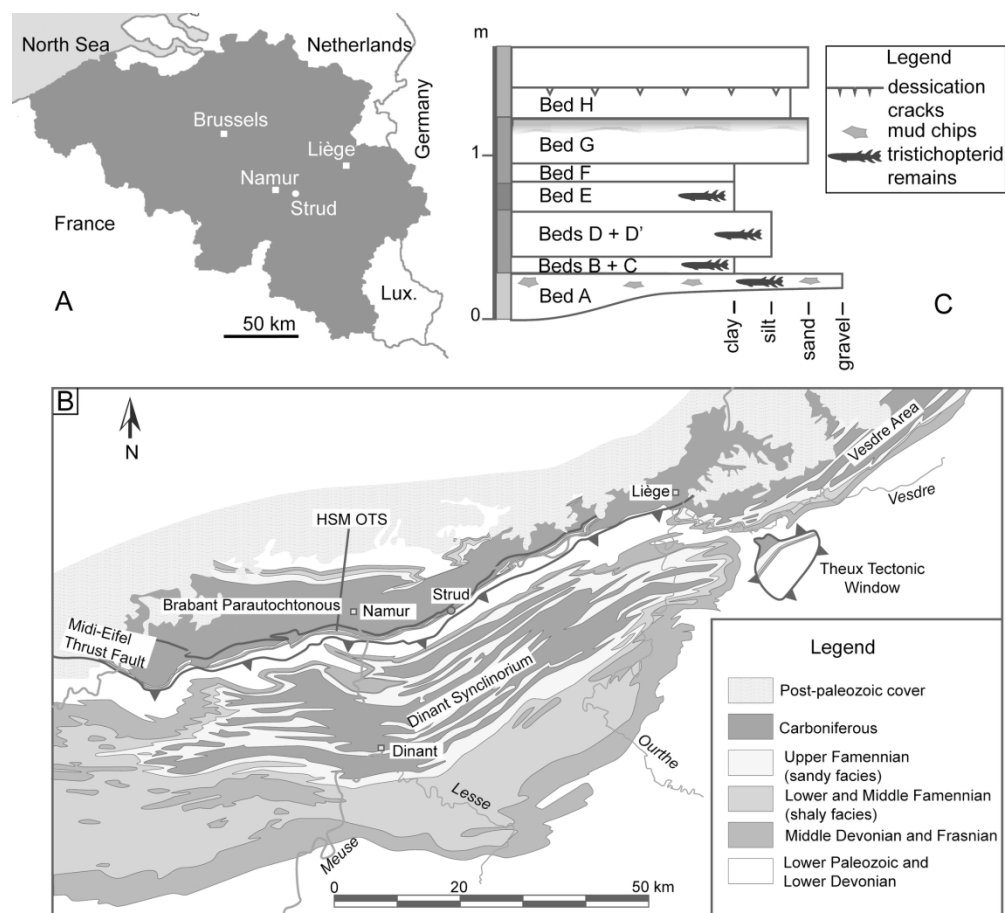


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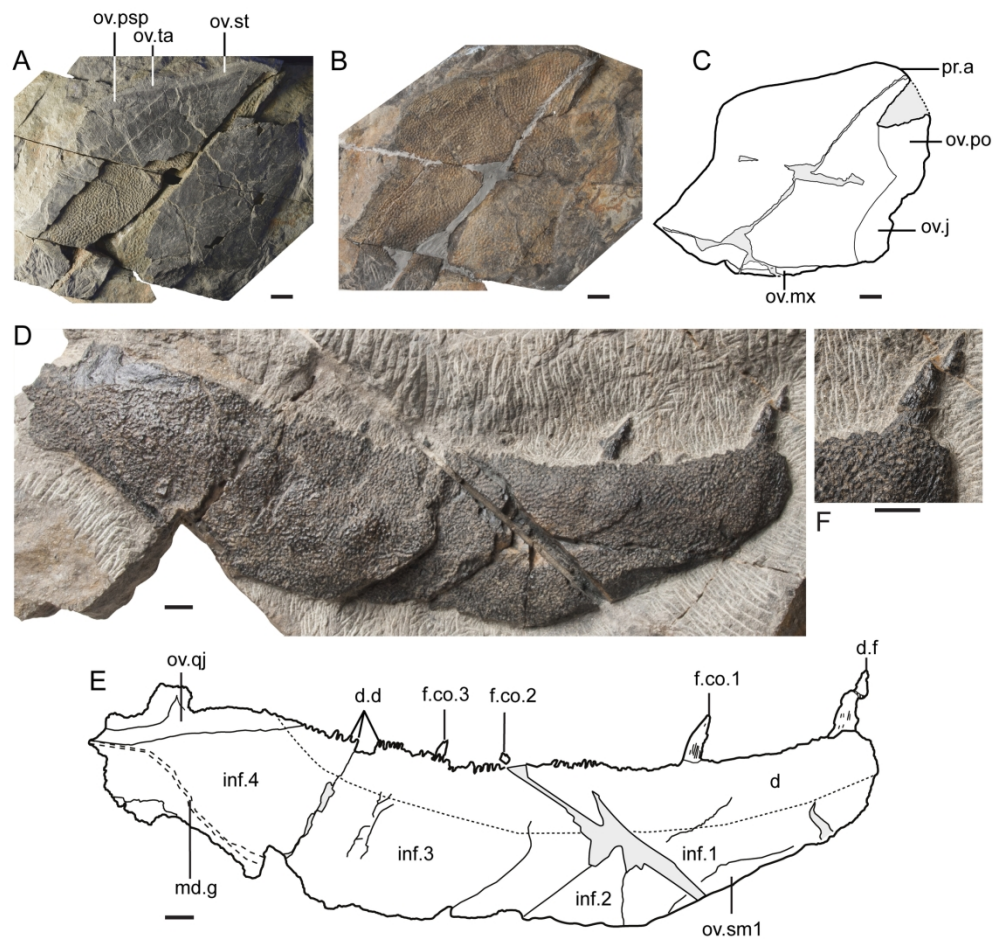


FIGURE 2. cf. *Langlieria socqueti*, Strud, Belgium, late Famennian. A, left squamosal, internal view, IRSNB P 9912, photograph; B, left squamosal, imprint of the external surface (bone removed), IRSNB P 9912, photograph; C, left squamosal, external view, IRSNB P 9912, interpretative drawing; D, right mandible, external view, IRSNB P 9913, photograph; E, right mandible, external view, IRSNB P 9913, interpretative drawing; F, right mandible, external view, IRSNB P 9913, close-up photograph on the symphysis. Scale bars equal 1 cm. [planned for page width]

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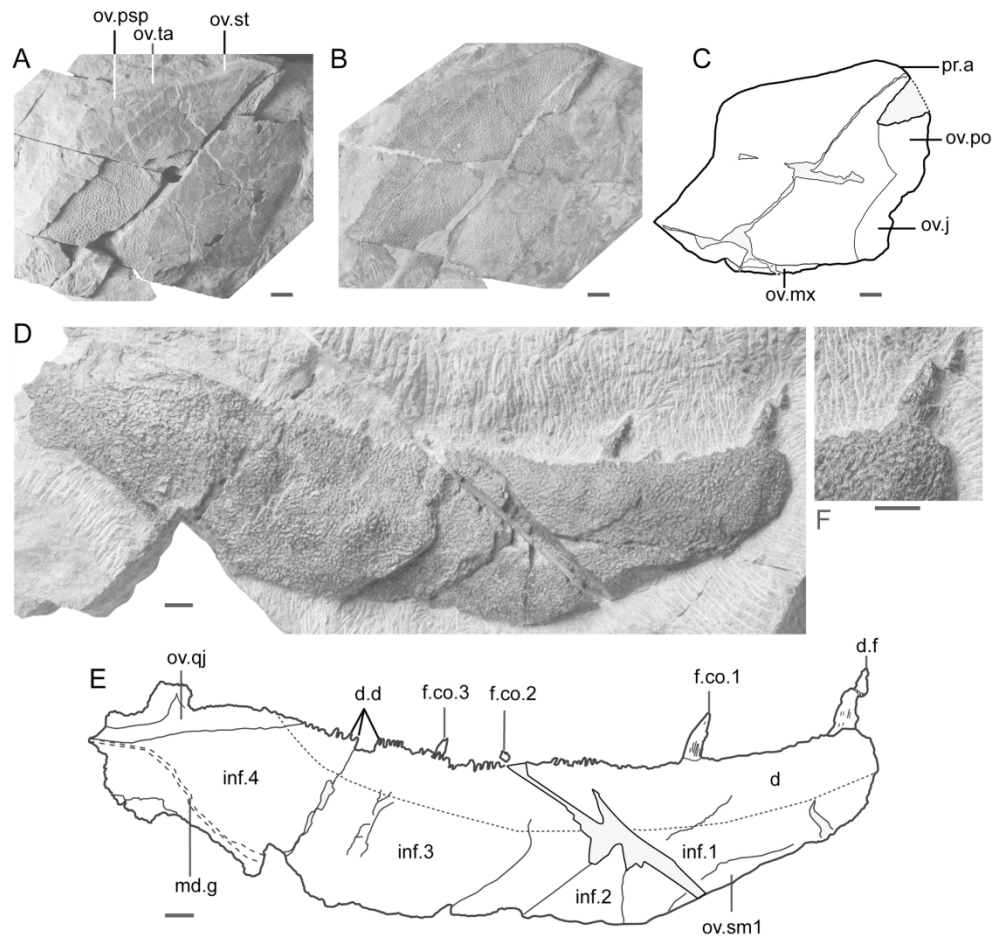


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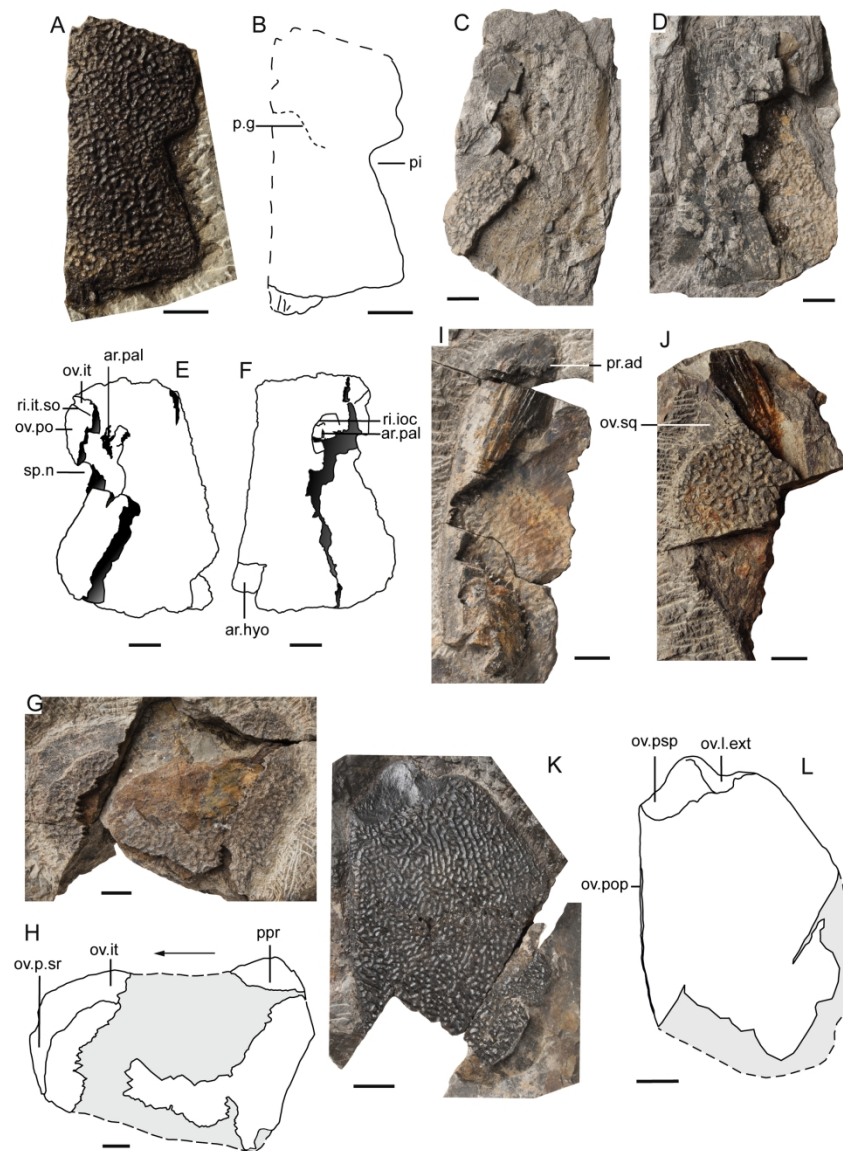


FIGURE 3. *cf. Eusthenodon wangsjoii*, Strud, Belgium, Upper Famennian. A, incomplete left parietal, external view, IRSNB P 9910, photograph; B, incomplete left parietal, external view, IRSNB P 9910, interpretative drawing; C–D, left supratermporal, external and visceral views, IRSNB P 9914, photographs; E–F, left supratermporal, external and visceral views, IRSNB P 9915, interpretative drawings; G, left postorbital, external view, IRSNB P 9915, photograph; H, left postorbital, external view, IRSNB P 9915, interpretative drawing; I–J, left preopercular, external and visceral views, IRSNB P 9916, photographs; K, left opercular, external view, IRSNB P 9917, photograph; L, left opercular, external view, IRSNB P 9917, interpretative drawing. Black arrow points anteriorly. Scale bars: A–H equal 1 cm, I–L equal 2 cm. [planned for page width]

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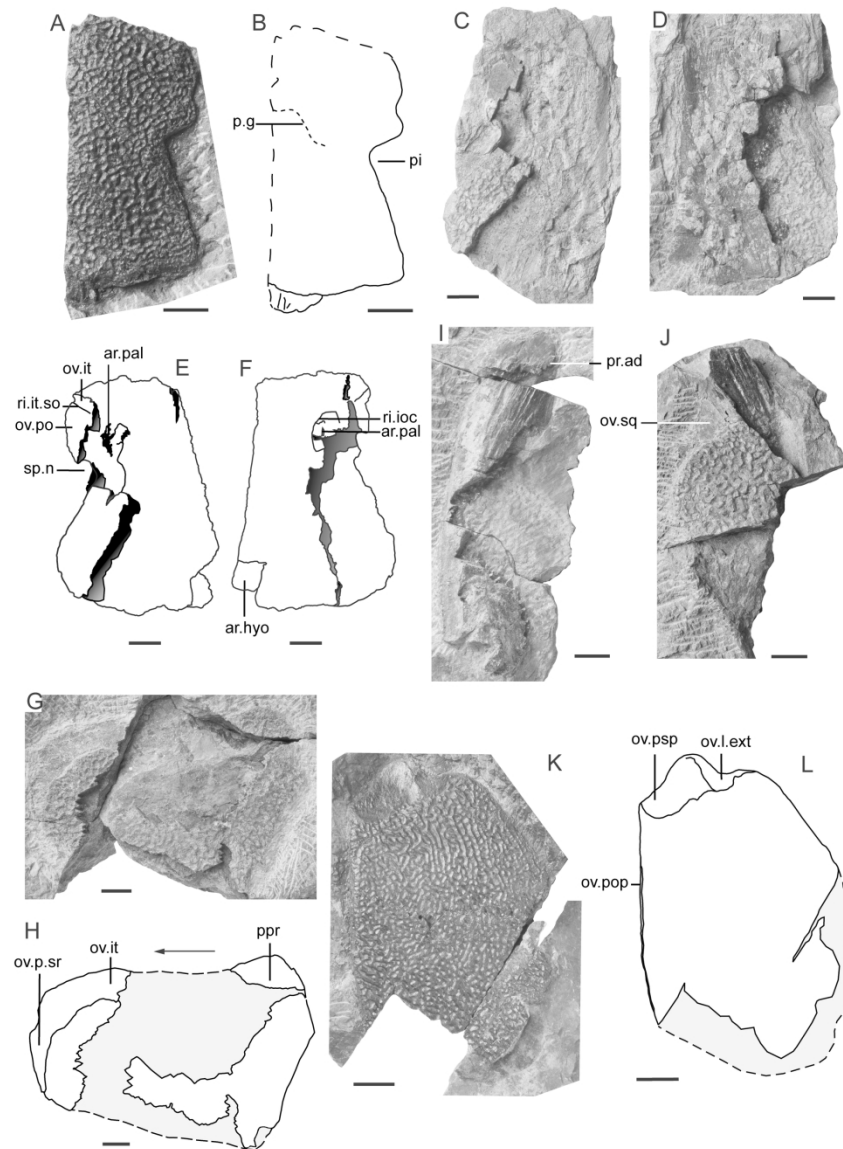


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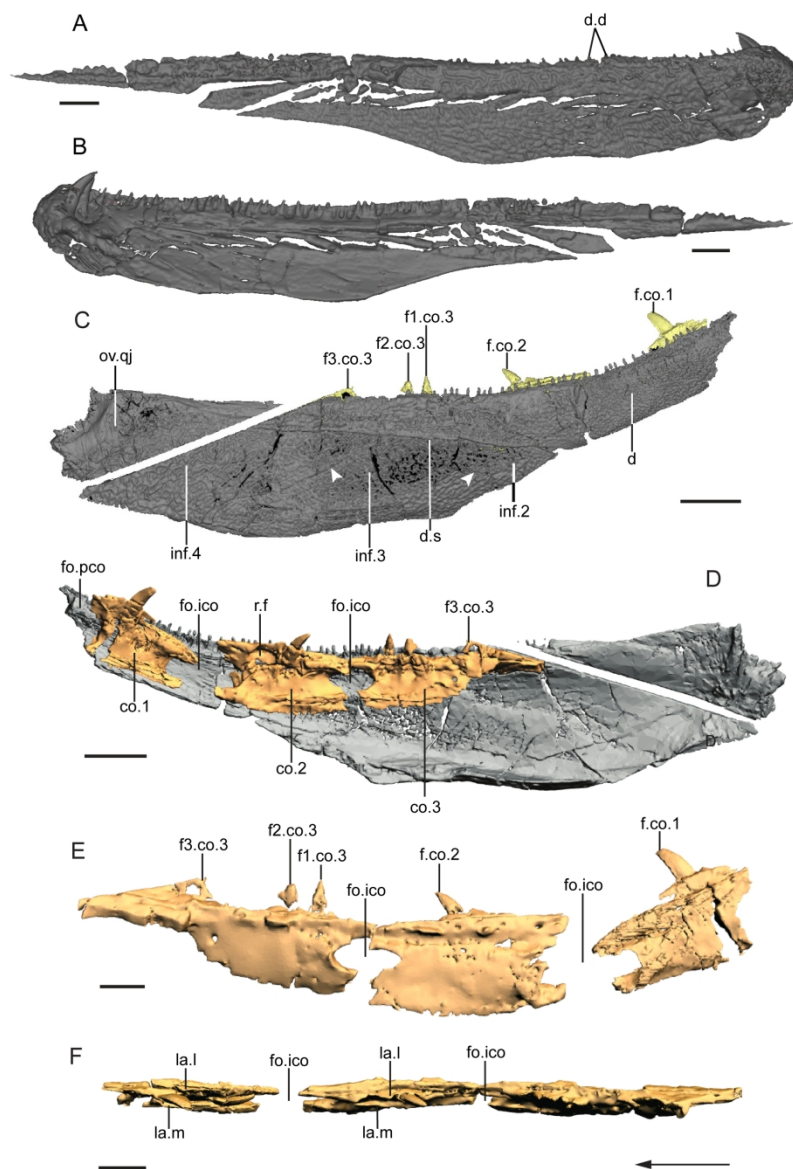


FIGURE 4. *cf. Eusthenodon wangsjoii*, Strud, Belgium, late Famennian. A, right dentary, external view, IRSNB P 9918, 3D reconstruction; B, right dentary, visceral view, IRSNB P 9918, 3D reconstruction; C, right mandible, external view, IRSNB P 9919, 3D reconstruction; D, right mandible, visceral view, IRSNB P 9919, 3D reconstruction; E, coronoids, external view, IRSNB P 9919, 3D reconstruction; F, coronoids, apical view, IRSNB P 9919, 3D reconstruction. Left white arrow indicates putative suture between the infradentaries 3 and 4, right white arrow indicates pit line of infradentary 2. Black arrow points anteriorly. Scale bars: A–B, E–F equal 1 cm, C–D equal 2 cm. [planned for page width]

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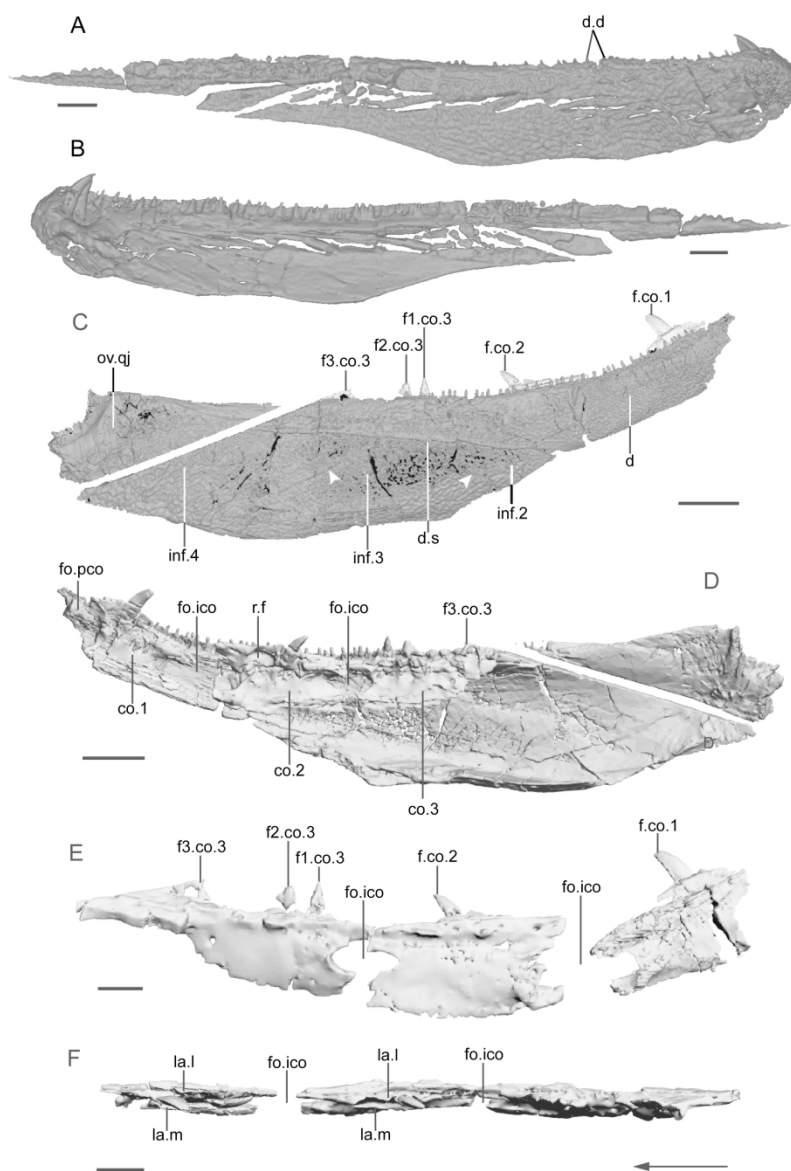


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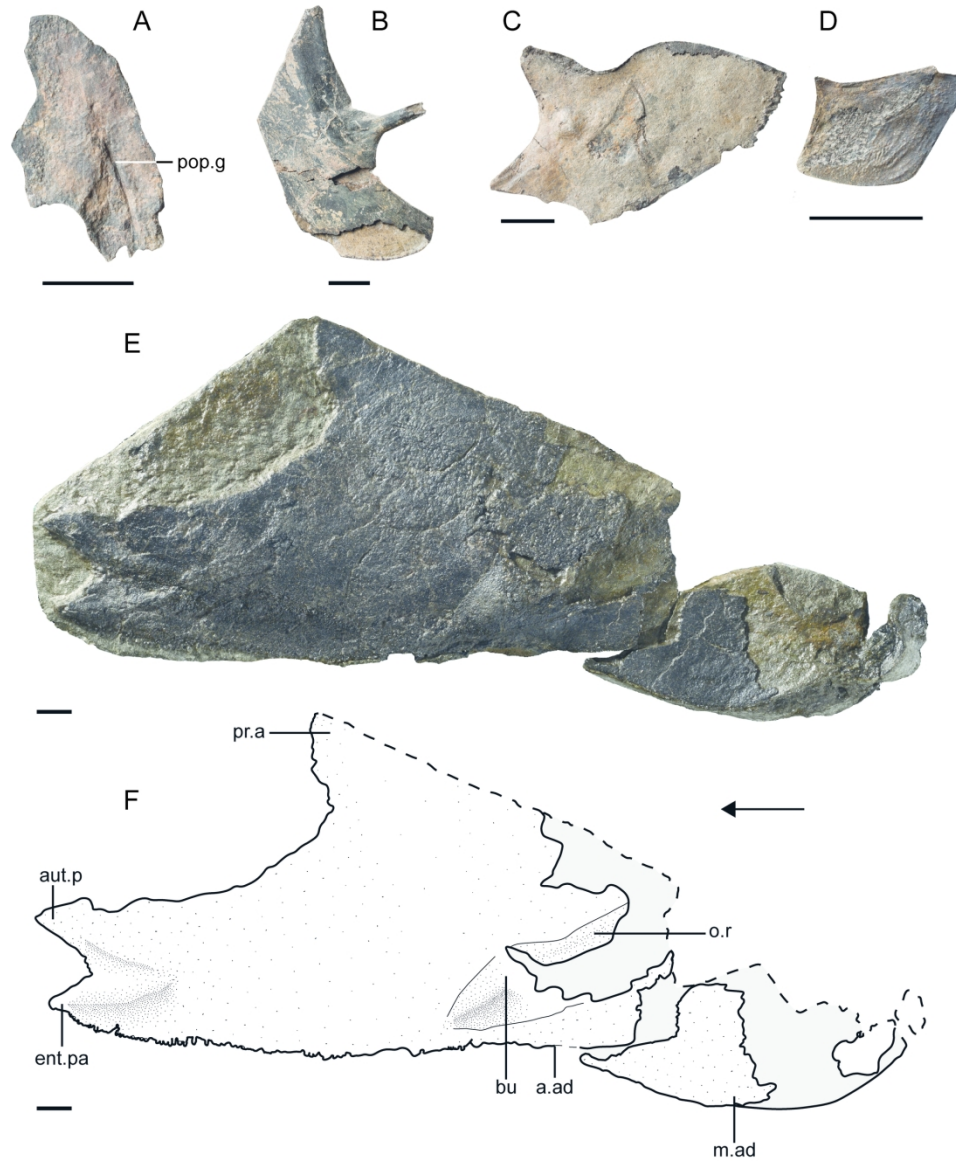


FIGURE 5. cf. *Tristichopteridae* indet., Strud, Belgium, Upper Famennian. A, right preopercular, external view, IRSNB P 9920, photograph; B, left subopercular, visceral view, IRSNB P 9921, photograph; C, left subopercular, visceral view, IRSNB P 9922, photograph; D, left subopercular, visceral view, IRSNB P 9923, photograph; E, right palatoquadrate, visceral view, IRSNB P 9911, photograph; F, right palatoquadrate, visceral view, IRSNB P 9911, interpretative drawing. Black arrow points anteriorly. Scale bars equal 1 cm. [planned for page width]

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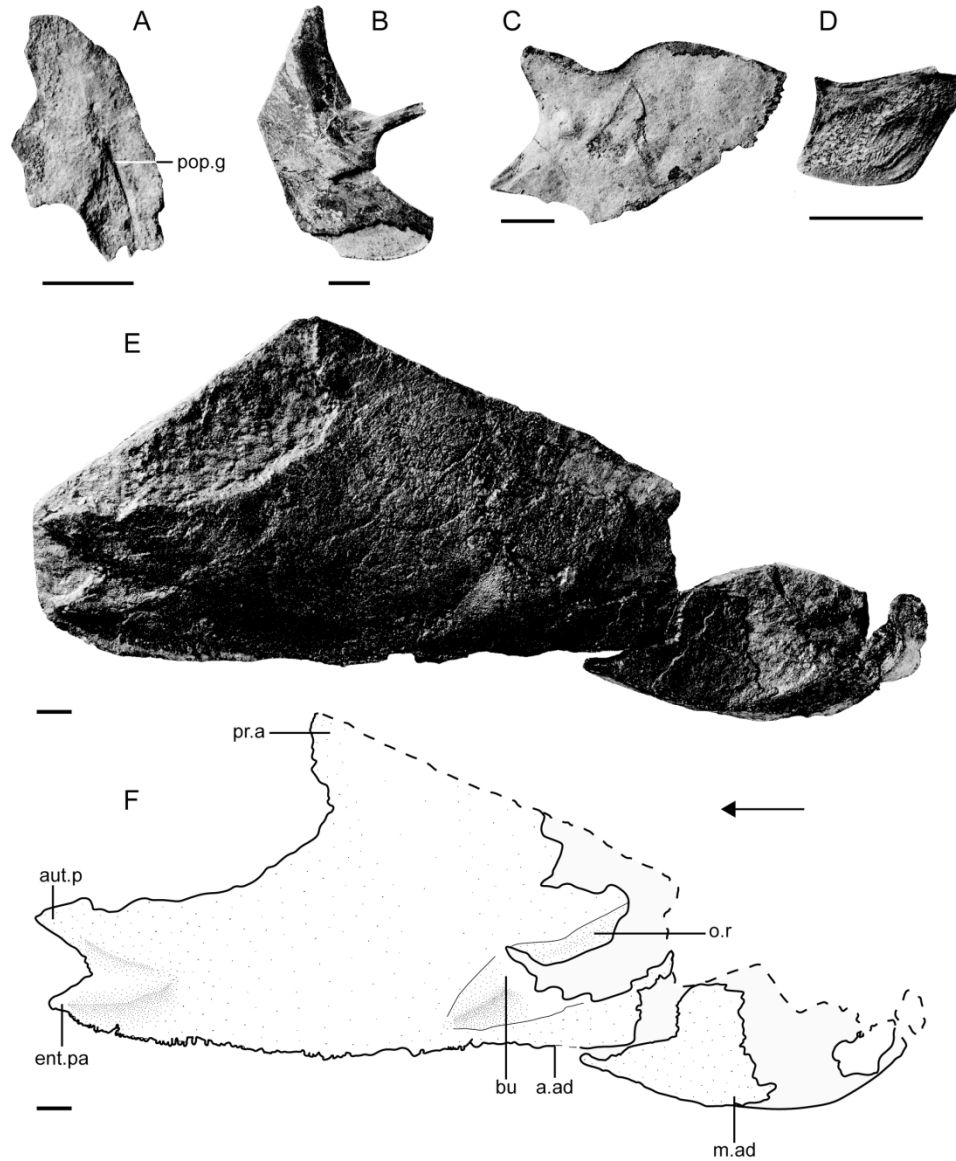


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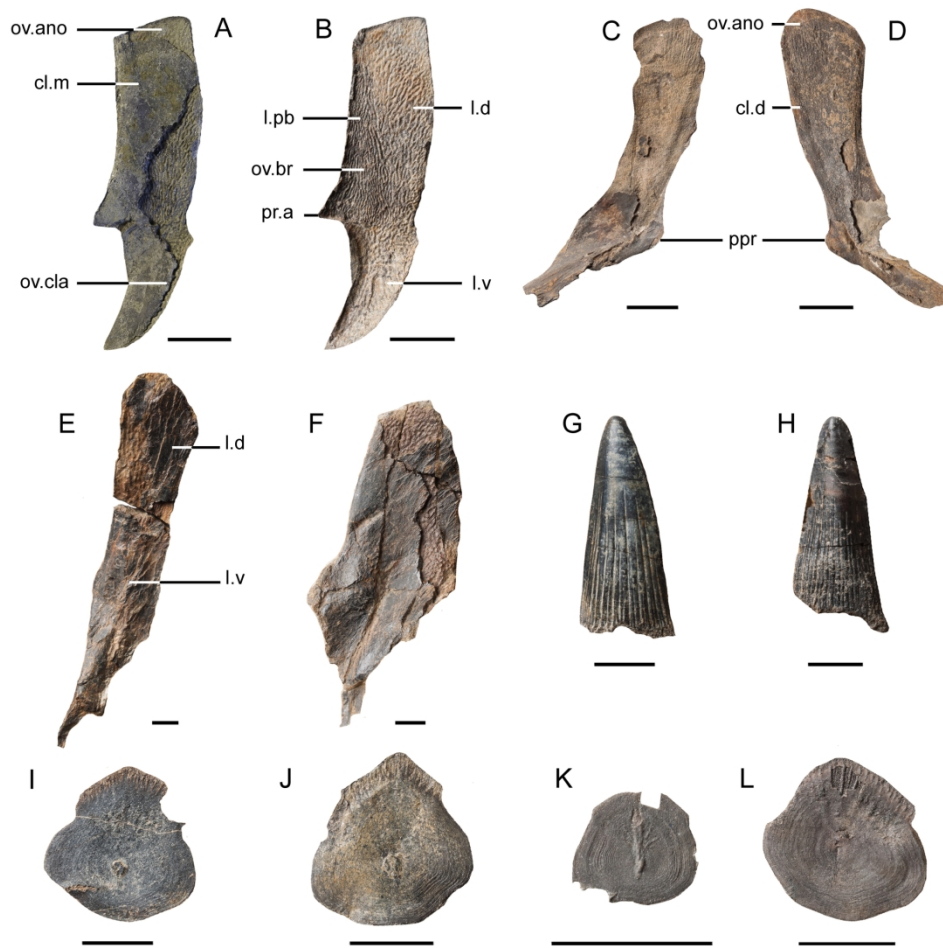


FIGURE 6. cf. *Tristichopteridae* indet., Strud, Belgium, Upper Famennian. A, right cleithrum, visceral view, IRSNB P 9924, photograph; B, right cleithrum, imprint of the external view (bone removed), IRSNB P 9924, photograph; C-D, right cleithrum, external and visceral views, IRSNB P 9925, photographs; E, incomplete right cleithrum, visceral view, IRSNB P 9926, photograph; F, incomplete right cleithrum, visceral view, IRSNB P 9927, photograph; G, isolated fang, labial or lingual view, IRSNB P 9928, photograph; H, isolated fang, labial or lingual view, IRSNB P 9929, photograph; I, isolated scale, visceral view, IRSNB P 9930, photograph; J, isolated scale, visceral view, IRSNB P 9931, photograph; K, isolated scale, visceral view, IRSNB P 9932, photograph; L, isolated scale, visceral view, IRSNB P 9933, photograph. Scale bars equal 1 cm. [planned for page width]

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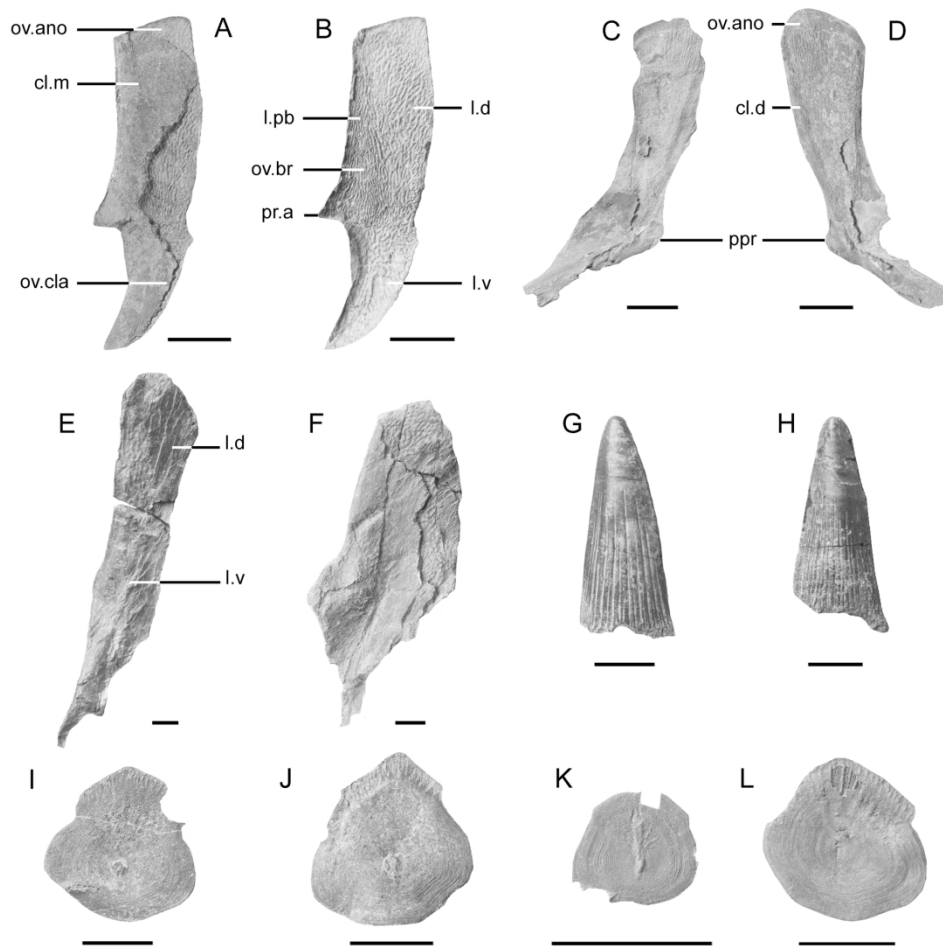


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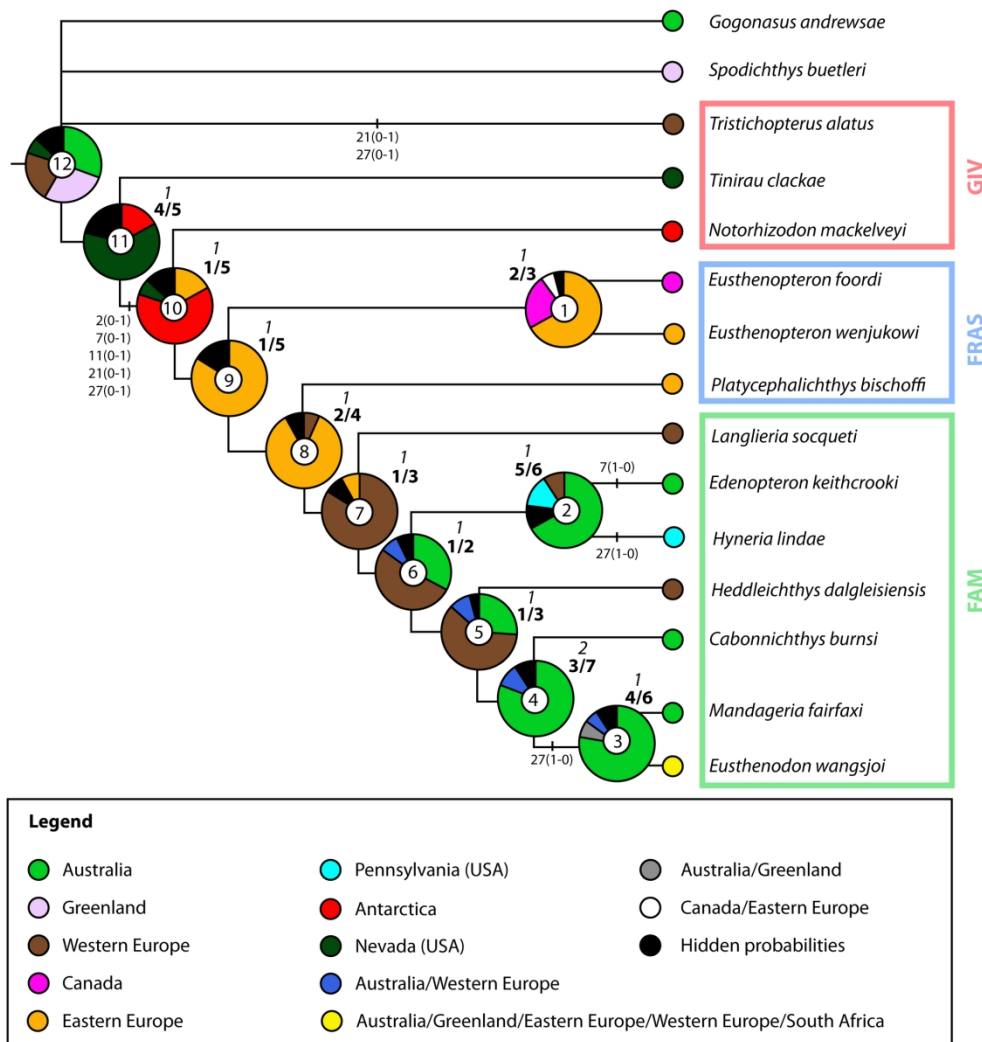


FIGURE 7. Strict consensus tree showing phylogenetic relationships of the Tristichopteridae, with maximum parsimony biogeographic reconstruction result using Bayesian Binary MCMC analysis mapped on. The number in the center of each pie chart corresponds to the node number. The pie chart over each node represents the probability that the clade originated from each continental area. The numbers on the top of each pie chart correspond to the Bremer index (in italics) and to the minimal and maximal number of synapomorphies at each node (in bold). Some character state changings have been reported on the branches. GIV for Givetian, FRAS for Frasnian and FAM for Famennian. [planned for page width]

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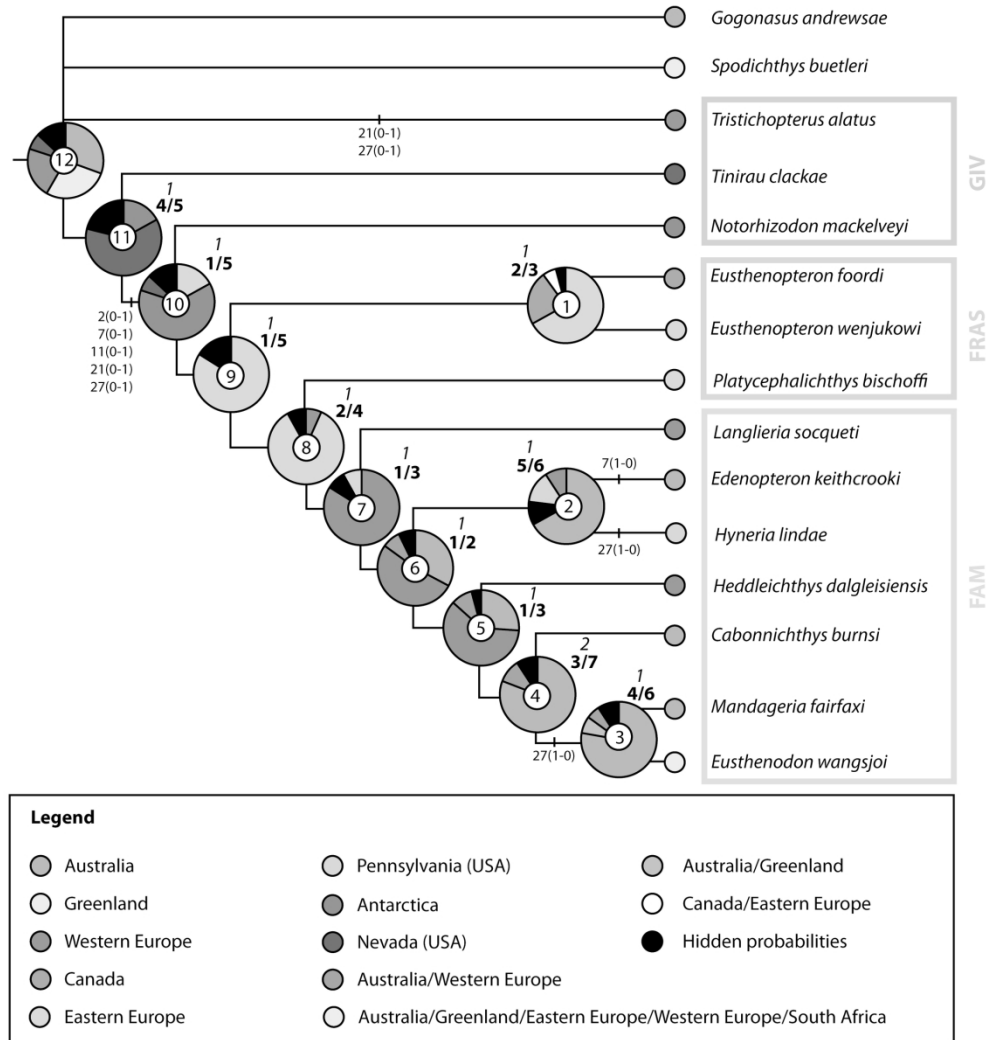


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