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A second species of *Tristichopterus* (Sarcopterygii: Tristichopteridae), from the Upper Devonian of the Baltic Region

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ABSTRACT

A review of the osteology of the tristichopterid sarcopterygian *Eusthenopteron kurshi* Zupinš, 2008, from the Lower Frasnian of Latvia, indicates that it should be placed in the genus *Tristichopterus*, and a new combination *Tristichopterus kurshi* Zupinš is proposed. The features that support this include: the number of coronoid fangs, proportions of the coronoids and the skull roof, and the relatively small epichordal lobe of the caudal fin. Recognition of a second species of *Tristichopterus* extends the stratigraphic range of the genus to the Upper Devonian, and its geographic range to the Baltic Region in northern Europe. □ *Eusthenopteron*, *Tristichopterus*, *Tristichopteridae*, *Devonian*.

Following excavation of well preserved sarcopterygian material from the Lower Frasnian, Lode clay quarry (Lode Formation) in Latvia; Zupinš (2008) erected the taxon *Eusthenopteron kurshi* on the basis of a complete individual and 12 partial remains. The species was interpreted to be the most primitive within the genus *Eusthenopteron*, on the basis of its more asymmetric caudal fin, and remarkably low parietal to postparietal shield length ratio: 1.57, compared to 1.7–1.85 in *E. foordi* Whiteaves, 1881, 1.85 in *E. traquairi* Westoll, 1937, and 1.95 in *E. savesoderberghi* Jarvik, 1937 (Jarvik 1950). A revision of the original description of the material, however, suggests that the material assigned to *E. kurshi* does not belong to *Eusthenopteron*, but to the genus *Tristichopterus*. Here I review the features that support referral of this species to *Tristichopterus*.

OBSERVATIONS

Several features of the material assigned to *Eusthenopteron kurshi* by Zupinš (2008) clearly suggest affinities to *Tristichopterus*, and also distinguish it from other species of *Eusthenopteron*. These are:

1. The posterior coronoid possesses a single pair of fangs. The only genus of tristichopterid that possesses a single pair of fangs on the posterior coronoid is *Tristichopterus* (Snitting 2008a).
2. In *Eusthenopteron* (and more derived tristichopterids), the posterior coronoid is around twice the length of the other two coronoids, whereas in *Tristichopterus* it is only approximately 35–40% longer (Snitting 2008a, b). In *E. kurshi*, the posterior coronoid is about half as long again as the anterior and middle coronoids (Zupinš 2008).
3. The available material of *E. kurshi* suggests a maximum length of 55 cm (Zupinš 2008). This small size corresponds better to a maximum length of 40 cm for *Tristichopterus* (Ahlberg & Johanson 1997). *Eusthenopteron* typically measures more than 60 cm long, sometimes more than 100 cm, and one specimen, W.661, figured by Andrews & Westoll (1970), is estimated to have measured about 1.5 m long.
4. The proportion of the epichordal lobe to the total height of the caudal fin in *Tristichopterus* is one quarter to one third

(Egerton 1861; Jarvik 1937), whereas in *Eusthenopteron* it is three sevenths (Jarvik 1937) (Fig. 1). In the holotype of *E. kurshi*, the epichordal lobe is comparable to that of *Tristichopterus alatus* Egerton, 1864 in terms of its proportions. Caution must be used when interpreting this feature, however, because taphonomic distortion can cause fin lepidotrichia to spread out to different degrees (Zupinš 2008).

5. The parietal to postparietal shield length ratio in *E. kurshi* is 1.57. This is closer to the shield length ratio in *T. alatus* which

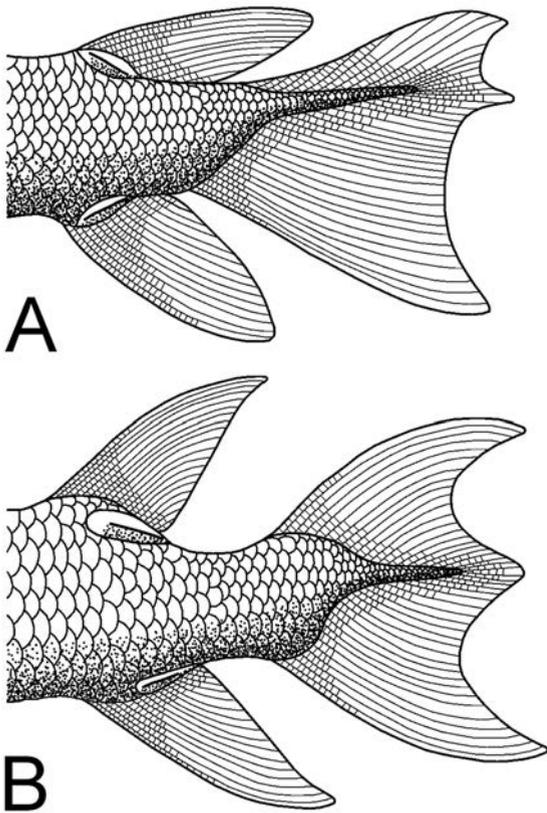


FIG. 1. Reconstructions of the morphology of the caudal region in left lateral view. A, morphology of *Tristichopterus*, characterised principally by a strongly heterocercal caudal fin; after Egerton (1861). B, morphology of *Eusthenopteron*, characterised principally by a near-homocercal caudal fin; after Jarvik (1980). Reconstructions not to scale.

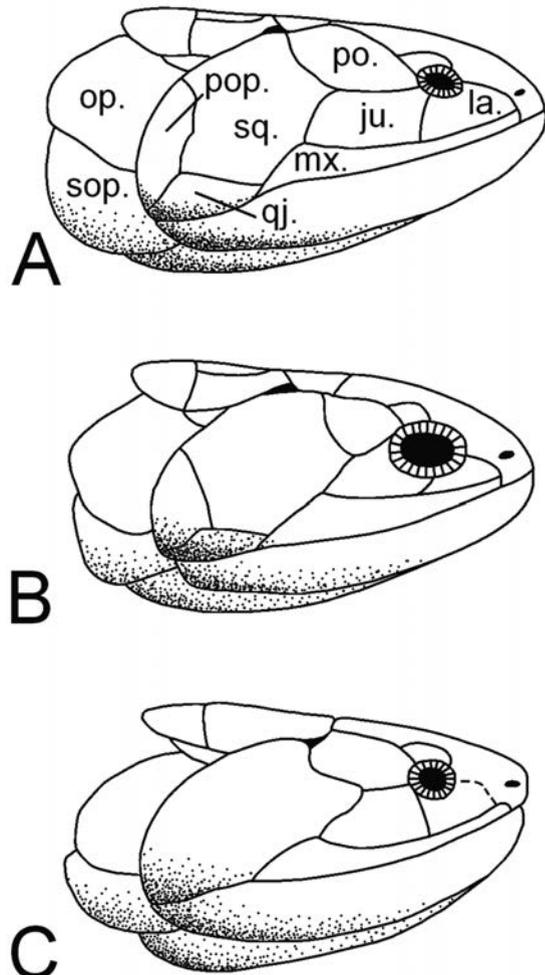


FIG. 2. Reconstructions of the skull, lower jaws and operculogular series in right lateral view. A, *Eusthenopteron foordi*, after Jarvik (1944). B, *Tristichopterus alatus*, mostly after Traquair (1875). C, *Tristichopterus kurshi*, based on the holotype, after Zupinš (2008); sutures of posterior cheek plate, parietal shield and postparietal shield unknown. Reconstructions not to scale. Abbreviations: ju., jugal; la., lacrimal; mx., maxilla; op., opercular; po., postorbital; pop., preopercular; qj., quadratojugal; sop., subopercular; sq., squamosal.

- is 1.4–1.49 (Jarvik 1937; Westoll 1937); in *Eusthenopteron*, it is 1.7–1.95 (Jarvik 1950).
6. The pineal foramen of *Eusthenopteron foordi*, and probably also *E. savesoderbergi*, is approximately level with the posterior margin of the orbits (Jarvik 1937, 1944). In both *E. kurshi* and *Tristichopterus* however, it is positioned behind the posterior margin of the orbits, by at least ten percent of the length of the parietal shield (Snitting 2008a; Zupinš 2008).
 7. In *E. foordi*, the opercular is of about the same height as the subopercular (Jarvik 1944), whereas in *Tristichopterus*, the former bone is around 1.5 times as high as the latter (Traquair 1875). In *E. kurshi*, the opercular is around twice as high as the subopercular (Zupinš 2008; Fig. 2).

Notwithstanding the many similarities to *Tristichopterus* and differences to *Eusthenopteron*, *E. kurshi* does show affinities with the latter genus. As in *E. foordi*, the orbits of *E. kurshi* are relatively small compared to the size of the head, in contrast to *Tristichopterus* where the orbits are large, relative to the size of the head (Traquair 1875; Jarvik 1944). The shapes of the postorbital and jugal in *E. kurshi* are different to those bones in *Tristichopterus*, but quite similar to those of *E. foordi* (Fig. 2; Traquair 1875; Jarvik 1944). Interestingly, the dorsal, pelvic and anal fins of *E. kurshi* are positioned more posteriorly than those of both *Tristichopterus* and *Eusthenopteron*, particularly the anterior dorsal and pelvic fins (Zupinš 2008), and in this regard it is distinguished from both genera.

On the basis of the above observations, *E. kurshi* is better placed in *Tristichopterus* than in *Eusthenopteron*. *Eusthenopteron kurshi* differs from the type species, *T. alatus*, in adult size, relative orbit size, cheek bone shape, fin positioning and vomer morphology (Snitting 2008a; Zupinš 2008) and a new combination *Tristichopterus kurshi* (Zupinš, 2008) is thus proposed.

SYSTEMATIC PALAEOLOGY

Class Sarcopterygii Romer, 1955

Order Osteolepiformes Berg, 1937

Family Tristichopteridae Cope, 1889

Genus *Tristichopterus* Egerton, 1861

Type species. *Tristichopterus alatus* Egerton, 1861.

Emended generic diagnosis. Small cosmine-free tetrapodomorph. Caudal fin heterocercal, trifurcate, epichordal lobe one quarter to one third the total height of the fin. Extratemporal bone posteriorly displaced, in 'postspiracular' position. Pineal foramen slightly posterior to posterior margin of orbit. Opercular greater in height (by at least fifty percent) than subopercular. One fang pair present on ectopterygoid and posterior coronoid. Posterior coronoid slightly (35–50%) longer than anterior and middle coronoids. Parasymphyseal dental plate small and drop-shaped, failing to contact anterior coronoid. Vomer possesses long posterior process, suturing with much of lateral edge of parasphenoid. Ethmosphenoid and otico-occipital of equal length. Crista parotica extended posteriorly; posterior margin of floor of fossa bridgei transverse, forming distinct posterolateral corner to otico-occipital.

Remarks. Since the discovery and original description of *E. foordi* (Whiteaves 1881), the great similarity between *Eusthenopteron* and *Tristichopterus* has been well recognised; indeed, the two are considered the most basal tristichopterid genera known (Clément *et al.* 2009). Doubt has previously surrounded the validity of the genus *Eusthenopteron* and whether it should be synonymised with the earlier named *Tristichopterus*, with several attempts to distinguish the two genera having been made (e.g. Traquair 1890; Jarvik 1937; Zupinš 2008). Only recently has the matter been satisfactorily resolved, in favour of their separation (Snitting 2008a). *Eusthenopteron* can be distinguished from *Tristichopterus inter alia* by the possession of two fang pairs on the ectopterygoid and posterior coronoid, a very long posterior coronoid (around twice as long as the anterior and middle coronoids), an ethmosphenoid which is longer than the otico-occipital and a more symmetric caudal fin. *Eusthenopteron* is also a distinctly larger fish than *Tristichopterus*; species of the former are typically longer than 60 cm (and often reach

considerably more, in excess of 1 m), whilst *Tristichopterus* is the smallest member of the Tristichopteridae, measuring less than 60 cm, and generally much less.

Tristichopterus kurshi (Zupiņš, 2008)
comb. nov.

Eusthenopteron kurshi Zupiņš, 2008: p. 40-46, figs 1-5.

Holotype. LDM G 291/23, complete skeleton, squamation and fins, as well as counterpart of posterior part of body. Lower Frasnian Lode Formation, Lode clay quarry, Latvia. LDM G denotes the Geology Collections, Natural History Museum of Latvia, Riga.

Material. Material of Zupiņš (2008).

Emended specific diagnosis. Tristichopterid of small size. Orbits relatively small compared to size of head. Vomers fused medially, their anteromedial corners extend anteriorly so as to form slightly convex anterior margin of vomer pair. Parietal shield approximately 1.6 times as long as postparietal shield. Dorsal margin of postorbital more or less straight, jugal-postorbital suture straight. Jugal forms near right angle around its contribution to orbit margin, formed from jugal-postorbital and jugal-lacrimal sutures; jugal contribution to orbit margin minimal. Squamosal extends significantly anterior to joint between parietal and postparietal shields. Opercular twice as high as subopercular. Dorsal, pelvic and anal fins positioned well posterior on body. Caudal fin heterocercal, epichordal lobe one third of total height of fin.

Remarks. Previously *Tristichopterus* was known only from the Middle Givetian of Scotland (Marshall *et al.* 2010). *Tristichopterus kurshi* now extends the stratigraphic range of the genus into the Lower Frasnian (but see Forey *et al.* 2000, who assigned a Late Givetian age to the Lode Formation), and also extends its geographic range to Latvia in northern Europe.

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