

A tristichopterid sarcopterygian fish from the upper Middle Devonian of Nevada

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(Received 20 January 2012; final version received 5 March 2012)

A new tristichopterid, †*Bruehnopteron murphyi* n. gen. n. sp., is described from the uppermost Givetian, Middle Devonian, from the Northern Simpson Park Range in central Nevada, USA. A complete morphological description is provided. The new tristichopterid is placed between †*Jarvikina* and †*Heddeleithys* in recently published phylogenetic diagrams of tristichopterid sarcopterygians. Shape of lacrimal and jugal and the longest preorbital region of all tristichopterids are unique features of the new form. The new tristichopterid has enlarged premaxillary ‘pseudofangs’ and anterior dentary fangs, features of ‘moderately derived’ tristichopterids.

Keywords: sarcopterygian fish; marine; Middle Devonian; Nevada, USA

Introduction

Reed (1979) described tristichopterid remains, which he collected at Red Hill, Nevada, in 1974–1975, as †*Eusthenopteron* in his unpublished Ph.D. dissertation and compared them with different species of †*Eusthenopteron*. That identification persisted in the literature until the end of the last century. New Red Hill material collected by the Kansas University (KU) crew in 1987 and prepared by L. Berner, Museum für Naturkunde, Humboldt Universität Berlin, revealed features that excluded the species from †*Eusthenopteron* (Schultze 2010, 2011). B. Swartz restudied Reed’s material in his Ph.D. dissertation and reached the conclusion that Reed’s material is closer to Elpistostegalia than to †Tristichopteridae (Elpistostegalia includes the Red Hill tristichopterid and all tetrapods after Swartz 2010). Here we will describe new material in the collections of the University of Kansas with material included in Reed’s dissertation to demonstrate that Reed correctly placed the form in the Tristichopteridae, even though we think it should be separated from †*Eusthenopteron*.

The upper Middle Devonian Red Hill locality was discovered by M. Murphy in 1966, and then excavated for fishes by the University of California, Riverside, in 1973 (Murphy et al. 1976), by the University of California, Berkeley in the 1970s (Gregory et al. 1977) and 1984, and by the University of Kansas, Lawrence, in the 1980s (Schultze 2010). The fish fauna of that locality is dominated by specimens of †*Asterolepis* sp. (Murphy et al. 1976). Reed prepared the material of Red Hill with acid, so that he had in hand mainly single bones like in the case of the tristichopterid material. In addition, there exists a large

acid-prepared tristichopterid specimen in the Berkeley collections, which is largely preserved intact. That specimen is part of Swartz’s Ph.D. dissertation. In contrast, the context of even disarticulated specimens is preserved by the old-fashioned needle-method of preparation.

The age of the Red Hill locality in the Northern Simpson Range, Nevada, is latest Givetian after the conodonts occurring with the fish within the lower *Klapperina disparalis* Zone (Johnson 1990: Fig. 52; Elliott and Johnson 1997; Elliott et al. 2000).

Materials and methods

The material described here was collected in 1974 and 1975 by the Berkeley crew, and in 1981, 1983 and 1987 (Figure 1) by the KU crew. The Berkeley crew checked breaks of the rocks for fossils in the field, then prepared the material by formic acid and treated it with Glyptal so that isolated specimens were extracted, which could be studied from all sides. The formic acid-prepared specimens present the ornamentation nicely. In contrast, the preferred field method of the KU crew was to split the rocks in the field to get an immediate impression of the preserved fossil. The material was later prepared by dental hammer and needle at the Paläontologisches Institut, Museum für Naturkunde, Humboldt Universität, Berlin, Germany (now, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin). In that way disarticulated specimens – as most of Red Hill specimens are – are kept together (see holotype of †*Bruehnopteron murphyi*, Figure 2(A)). The specimens were drawn with camera lucida, attached to a Wild M4 microscope (at KU).

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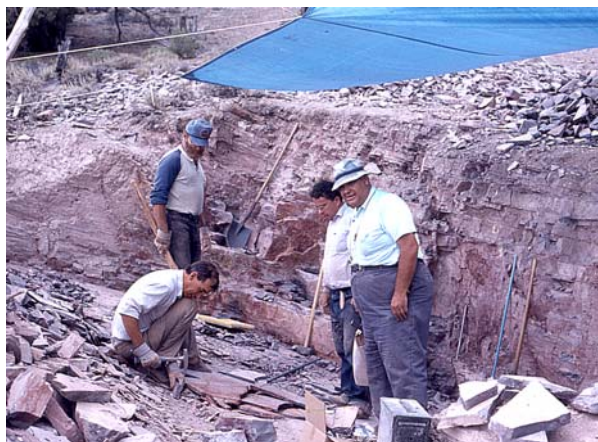


Figure 1. Red Hill (Northern Simpson Range, Nevada) excavation July 1987, from left to right: Erich Thomas (Herbede, Nordrhein-Westfalen, Germany), standing John Chorn (Lawrence, Kansas, USA), Peter Brühn (Essen, Nordrhein-Westfalen, Germany), and Keith Rigby Sen. (Provo, Utah, USA).

Photographs were taken by a conventional camera and by a digital camera.

We follow here the terminology corresponding to the bone homology with tetrapods (Westoll 1938, 1940; Jollie 1962; Schultze 2008).

Institutional abbreviations

KUVP, Vertebrate Paleontological collections, Museum of Natural History, and Biodiversity Institute, The University of Kansas, Lawrence, Kansas, USA.

MHNM, Musée d'Histoire naturelle de Miguasha, Quebec, Canada

SMNH, Paleozoologiska sektionen, Naturhistoriska Riksmuseet, Stockholm, Sweden

UCMP, Museum of Palaeontology, University of California, Berkeley, California, USA.

Systematic palaeontology

Osteichthyes Huxley 1880

Sarcopterygii Romer 1955

Choanata Säve-Söderbergh 1934 (sensu Schultze 1991)

Family †Tristichopteridae Cope 1889

Diagnosis (from Snitting 2008a, p. 26)

One unique character (extratemporal drop-shaped and in a postspiracular position) and several widely distributed characters (no cosmine, round scales with an internal boss, anteriorly positioned crescent-shaped parietal pit lines, small kite-shaped parasymphysial dental plate, a transverse posterior margin of the floor of the fossa bridgei, vomers with posterior processes that suture the lateral face of the parasphenoid, an elongate posterior coronoid and a triphycercal caudal fin).

†*Bruehnopteron* n. gen

Type and only species: †*B. murphyi* n. sp

Age and location: Middle Devonian, western USA

Etymology

The genus name is a composite of the name Bruehn and *pter*, Greek = wing. Peter Brühn, Essen, Germany, was an active field assistant during two field seasons in Nevada. He joined the KU crew at his own expense.

Diagnosis

The genus is uniquely characterised by an elongated lacrimal, an oval-shaped jugal, a postero-ventral elongated squamosal, a deep and narrow preopercle, a small quadratojugal and the longest preorbital region among tristichopterids. Postorbital and jugal bones at the posterior orbital border, supraorbital bone without posterior process beyond orbit, no accessory vomers and possession of marginal teeth on coronoids place †*Bruehnopteron* within basal tristichopterids. Characters like the posterior coronoid with two fangs and much longer than the penultimate coronoid, the position of the pineal foramen well behind the orbits and the possession of fangs on the anterior dentary and on the premaxilla, together with the lack of cutting edges on fangs and the lack of a kite-shaped pineal place †*Bruehnopteron* between †*Jarvikina* and †*Heddeleithys*.

†*Bruehnopteron murphyi* n. sp

1976 Rhipidistian: Murphy et al., p. 468

1977 *Eusthenopteron* cf. *foordi*: Gregory et al., p. 116

1996 *Eusthenopteron*: Schultze and Cloutier, p. 360, 368

1996 *Eusthenopteron* cf. *foordi*: Cloutier et al., p. 209, 211

2000 *Eusthenopteron foordi*: Elliott et al., p. 291

2000 *Eusthenopteron*: Elliott et al., p. 294: Fig. 1

2000 *Eusthenopteron* sp. cf. *E. foordi*: Elliott et al., p. 302

2010 tristichopterid rhipidistian n. gen, n. sp.: Schultze, p. 7: Fig. 6

2010 tristichopterid: Swartz, p. 173A

Holotype

KUVP 94040, left lateral side of the head, postparietal shield and cleithra. Figures 2(A),(B), 3 and 9(A),(B); Schultze (2010: Fig. 6).

Referred material

UCMP 117884, parieto-ethmoidal shield, Figures 5–7; Reed (1979, plate 59: Fig. 1–2, plate 60: Fig. 1–3, plate 61: Fig. 1–3, plate 62: Fig. 1–4); UCMP 118283, parieto-ethmoidal shield, Figure 4; Reed (1979, plate 63; Fig. 1–2);

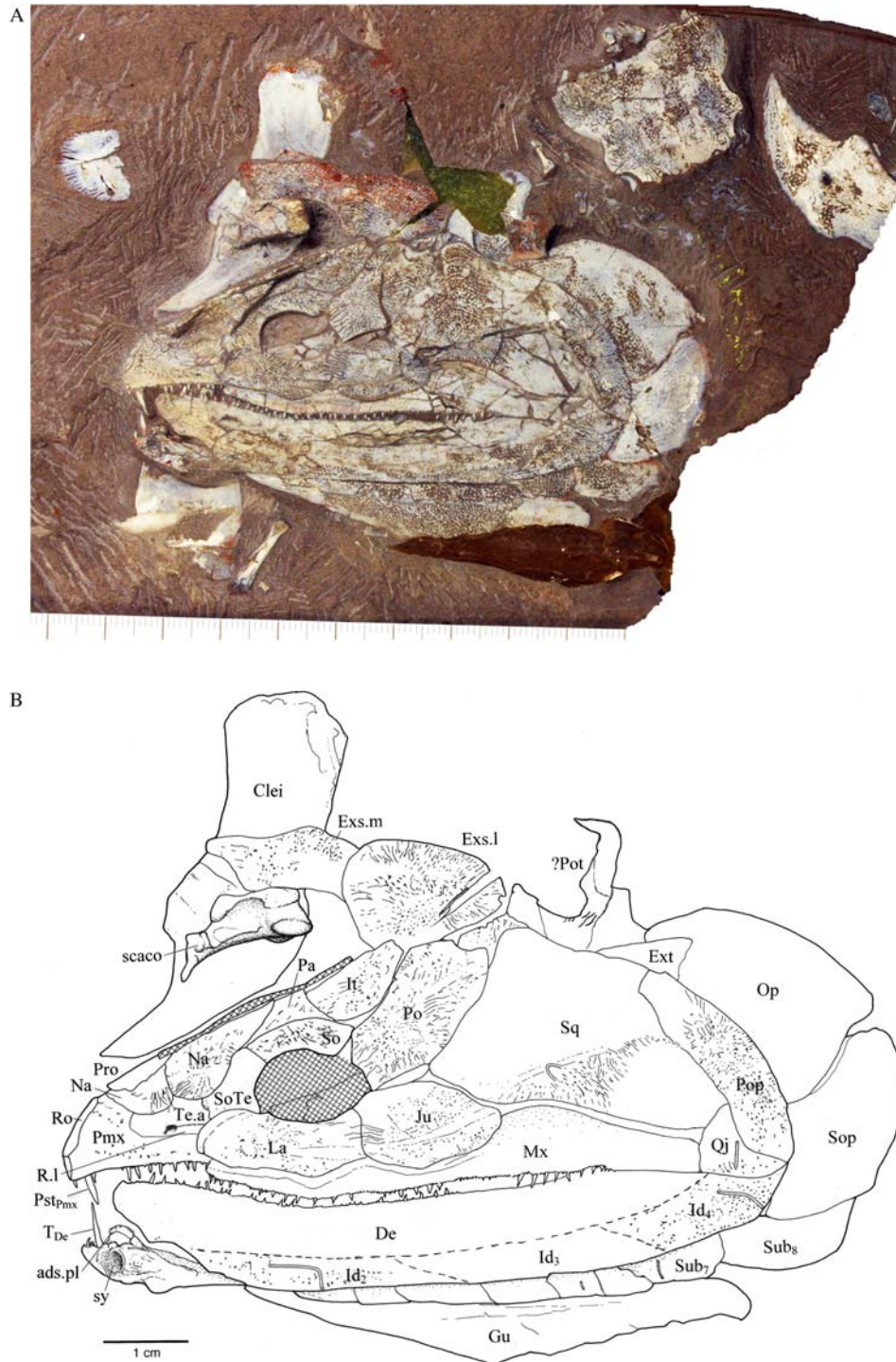


Figure 2. Holotype of †*B. murphyi* n. sp., (A) photograph of whole block with specimen KUV 94040, scale in cm and mm, (B) Lateral view of KUV 94040, scale equals 1 cm. Abbreviations: ads.pl, adsympysial plate; Clei, cleithrum; De, dentary; Exs.l, lateral extrascapula; Exs.m, median extrascapula; Ext, extratemporal; Gu, gular; Id_{1,2,3,4}, infradentary 1-4; It, intertemporal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Op, opercle; Pa, parietal; Pmx, premaxilla; Po, postorbital; ?Pot, questionable posttemporal; Pp, postparietal; Pro, postrostral; PstPmx, premaxillary 'pseudofang'; Qj, quadratojugal; R.l, lateral rostral; Ro, rostral; scaco, scapulocoracoid; So, supraorbital; Sop, subopercle; SoTe, supraorbito-temal; St, supratemporal; Sub_{7,8}, submandibula 7, 8; sy, symphyseal groove for contact of Meckelian cartilages; Ta, tabular; T_{De}, tusk on dentary; Te.a, anterior tectal.

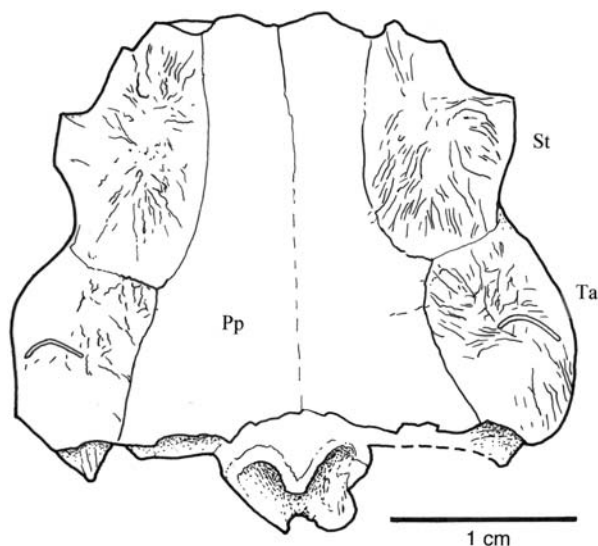


Figure 3. Postparietal shield of †*Bruehnopteron murphyi* n. sp., KUV 94040, in dorsal view. Abbreviations: Pp, postparietal; St, supratemporal; Ta, tabular.

UCMP 123135, left lower jaw, Figure 8; Reed (1979, plate 63; Fig. 3–5). This material is referred by Swartz (2012) to his new genus and species even though it compares in size to the holotype described here. In contrast the holotype of his species is much larger.

Type locality and horizon

Southwest flank of Red Hill at the northern end of the Northern Simpson Park Range, northwest of Eureka, Nevada (NW $\frac{1}{4}$, NE $\frac{1}{4}$, section 17, T.25N, R.50E on the Horse Creek Valley 15-minute Quadrangle in Eureka County, Nevada; or 40°03'34" N and 116°02'07" W); lower *K. disparalis* Zone, uppermost Givetian, Middle Devonian.

Etymology

The species name honours Dr M. Murphy, the discoverer of the Red Hill locality in the Northern Simpson Park Range, Nevada, who introduced the senior author and colleagues at Berkeley to this and other Devonian fish localities in the area. He supported the KU field crew staying at the field camp of the University of California, Riverside in the Roberts Mountains while we used their facilities. Mike Murphy, a specialist on the Devonian of Nevada, was at University of California, Riverside at that time.

Diagnosis

See diagnosis of genus, only species.



Figure 4. Parieto-ethmoidal shield of †*Bruehnopteron murphyi* n. sp., UCMP 118283, in dorsal view. Scale equals 1 cm.

Description

The head in lateral view, the postparietal shield in dorsal view and both cleithra in lateral and internal views are preserved in the holotype, KUV 94040 (Figure 2). The left lateral side of the head is more or less intact, whereas the skull roof is separated, so that the postparietal shield lies separately together with the left cleithrum. The right cleithrum lies above the anterior part of the head; it is covered partly by bones of the posterior skull roof. There are two parieto-ethmoidal shields in the Berkeley collection (UCMP 118283 and UCMP 117884), and one lower jaw (UCMP 123135), which are assigned to the new species and included in this description.

Ornamentation covers the surface of all head bones. It is composed of low tubercles, which anastomose to form short ridges; no regular pattern is obvious. The small specimen UCMP 118283 has almost as coarse tuberculation as does the larger one, and is therefore comparatively rough. The density of the tubercles is fairly constant throughout. Some tubercles have crater-like pits excavating their tops, or, more rarely, their sides.

Skull roof

The skull roof can be combined from isolated parieto-ethmoidal shields and the separated postparietal shield of the holotype. Bones above the lateral side of the holotype may represent the extrascapular series of the posterior end of the skull roof. The postparietal shield of the holotype (Figure 3) shows the postparietals, supratemporals and tabulars. The sutures between the bones are visible. The postparietal bones widen from anterior to posterior to little more than the double width. The separating median suture is only visible in the anterior 40%. The postparietals are flanked by nearly equally sized tabular and supratemporal bones. The right tabular bone forms an elongated oval, whereas the left has a straight medial and a convex lateral border; the tabular bones carry the arched lateral part of the postparietal pit line, which is not developed on the postparietal bones. The supratemporal bone shows anteriorly the invagination for the intertemporal, antero-laterally the invagination for the postorbital bone and forms laterally – together with the anterior part of the tabular bone – the invagination for the spiracular slit. The attachment area for the parieto-ethmoidal shield reaches from the anterior margin of the postparietal bones to the medial part of the anterior margin of the supratemporal bones.

There are two parieto-ethmoidal shields in the Berkeley collection, which were included in Reed (1979). They do not show the sutures between bones, like the postparietal shield, even though the ornament is identical on both shields. In addition, the branches deviating from the lateral-line system are not visible like in the postparietal shield and in the lateral face of the holotype. The smaller, 3.4 cm-long parieto-ethmoidal shield, UCMP 118283 (Figure 4), is more complete in dorsal view than specimen UCMP 117884; it lacks some bone in the area of the left lateral rostral and the right supraorbito-tectal. The larger, 12.8 cm-long specimen, UCMP 117884 (Figure 5), lacks bone on both sides in the supraorbito-tectal region. The most anterior portion overhangs the tooth-bearing margin slightly (Figure 6). In dorsal view, the anterior part of the parieto-ethmoidal shield has straight converging sides which meet to form a gently rounded tip. The central posterior part represents the parietals. The median suture between both parietals is visible in specimen UCMP 118283 between the posterior margin of the shield and the pineal foramen, which lies about one-fourth of the distance between the posterior and anterior margins of the shield. It lies posterior to the posterior extent of each parietal pit-line in specimen UCMP 11784, but between the posterior parts of the pit limbs in specimen UCMP 118283. The pineal foramen forms an elongated hole. There is some variation in the course of the pit-lines from right to left in both specimens and between the specimens. The right side of the posterior parieto-ethmoidal shield resembles the left in general

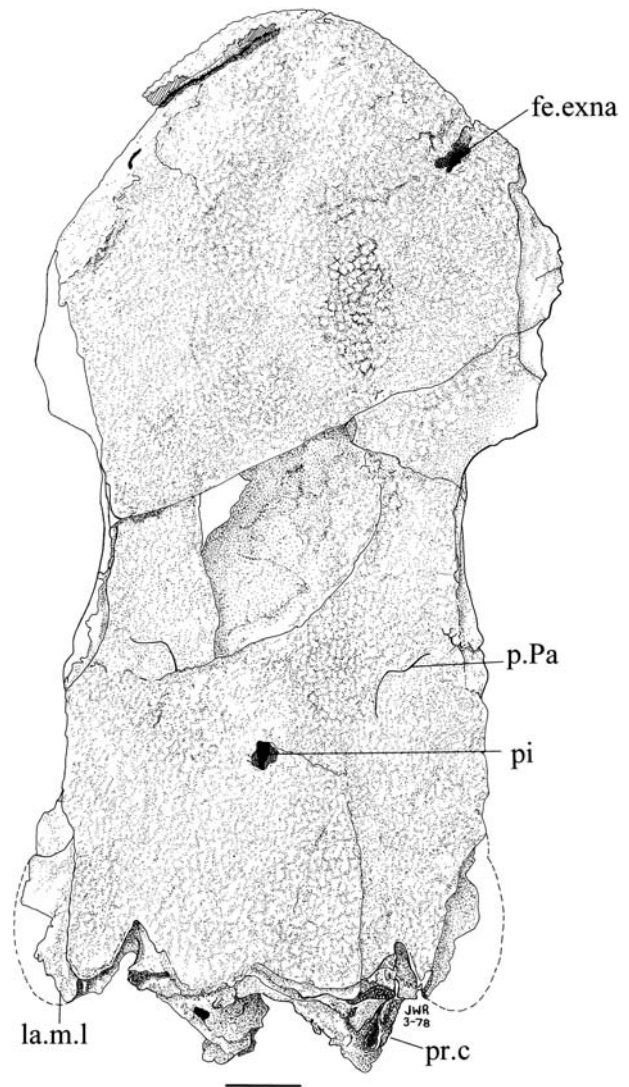


Figure 5. Parieto-ethmoidal shield of †*Bruehnopteron murphyi* n. sp., UCMP 117884, in dorsal view. Scale equals 1 cm. Abbreviations: fe.exna, fenestra exonarina; la.m.l, main lateral lamina of intertemporal; pi, pineal foramen; p.Pa, parietal pit line; pr.c, processus connectens.

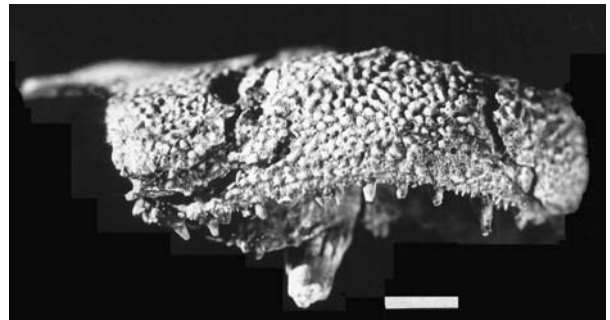


Figure 6. Parieto-ethmoidal shield of †*Bruehnopteron murphyi* n. sp., UCMP 117884, in anterior view. Scale equals 1 cm.

structure, but there are differences in detail. The grooves and ridges on the dorsal surface of the intertemporal bone are better defined on the right side of the shield. The edges of these structures are distinctly rounded. The shelf on the lateral side of the postero-lateral process is wider.

The parieto-ethmoidal shield is widest immediately in front of the orbits. The postorbital part is relatively long and straight sided. It includes the supraorbital bone that extends on the left side and forms the antero-dorsal margin of the orbit. It forms a short and slightly concave part of the antero-dorsal orbital margin. Posterior to the supraorbital bone follows the invagination for the supraorbital bone, which is not preserved in this specimen but in the holotype. The tooth-bearing margin is weakly concave and terminates at a sharp notch postero-ventral to the fenestra exorina. This notch excavates part of the lateral rostral and tectal bone.

The posterior margin of the supraorbital bone and the lateral margin of the parietal bone have a complicated surface against which the supraorbital articulates. Three laminae exist here. The dorsal lamina is the shortest; it is weakly concave in dorsal view and overhangs a groove at the base of the lamina. The overhang is most prominent anteriorly. The ventral lamina begins anterior to the posteriormost extent of the dorsal lamina, which is also concave in dorsal view, and its margin is directed laterad at its posterior end. The middle lamina branches off from the ventral lamina anteriorly and rises posteriad until it disappears just before reaching the posterior end of the dorsal lamina. Since no sutures can be distinguished in the UCMP specimens, it is uncertain whether these overlapped areas extend onto the intertemporal bone.

The areas overlapped on the posterior half of the intertemporal bone are slightly different on each side; on the right side the dorso-lateral lamina runs approximately straight posteriad until it is over the opening of the temporal sensory canal. It is then directed medially and continues as a weakly concave line to the posterior lateral corner of the bone. The dorso-lateral lamina is anteriorly weakly concave on the left side, and reaches an inflection point immediately anterior to the opening of the temporal sensory canal. This lamina overhangs the overlapped area throughout its length, but does so most prominently on its anterior half. The opening of the temporal sensory canal is markedly overhung by the dorso-lateral lamina, and on the right side this opening is backed by a short, laterally projecting buttress. Behind this buttress the surface is hollowed out in a hemispherical fashion, and is pierced by numerous foramina. On the left side there is no buttress and as a result the bone surface is merely concave in the lateral direction. Fewer foramina are present here. Near the posterior corner of the intertemporal bone, both sides show several short ridges directed slightly postero-laterally; on the left side they are more or less confined to the laterally

facing surface overhung by the dorsal lateral lamina. On the right side they extend farther laterally.

On the left side of the intertemporal bone, the main lateral lamina is divided into two parts. The ventral one is weak anteriorly. It is gently concave dorsally in lateral view, and concave anteriorly in dorsal view; it then curves back medially before joining with the dorsal part of the main lamina. There is a low ridge extending medially from the edge of the dorsal lateral lamina anterior to the opening for the temporal sensory canal. The dorsal part of the main lateral lamina of the intertemporal bone appears lateral to the infraorbital sensory canal opening. Anteriorly it is almost straight for a short distance. It then swings sharply laterad and is concave anteriorly in dorsal view. This lamina strongly overhangs the ventral part of the main lateral lamina before the two merge. The lateral margins are broken posteriorly, but a wide, more or less flat, overlapped surface appears to have been formed. The main lateral lamina is almost entirely missing on the right side.

The outline of the posterior margin of the parieto-ethmoidal shield is complicated. On the left side, the ornamented surface of the intertemporal bone overhangs the overlapped areas. The postero-lateral corner is blunt. There is a shelf just below the ornamented edge following the margin. The posterior margin of the intertemporal bone is deeply incised on both the ornamented and overlapped surfaces. The overlapped surface shows a narrower incision in the same place. The margin of the ornamented surface moves back sharply postero-medially from the apex of the notch. This margin reaches an angle and then moves medially as a wavering line to the midline, where another anteriorly directed notch is formed.

In the region of the postero-lateral corner, the overlapped surface of the intertemporal bone exhibits a series of low ridges and deep grooves oriented perpendicular to the posterior margin. The middle of these grooves is the deepest, and houses an opening for the temporal sensory canal. The margin of the overlapped area is blunt, and curves around and forms a deeply incised notch. The margin is directed almost straight posteriad on the medial side of this notch, and then bends abruptly at a transversely oriented joint. These two areas near the posterior margin of the parieto-ethmoidal shield are points of articulation between the neurocranium and the dermal bones.

The overlapped area of the parietal bone has a number of shallow grooves oriented perpendicular to the transverse axis. The width of the overlapped area is drastically reduced medial to the posteriorly projecting process of the intertemporal bone; it becomes a mere shelf, thinning to an edge posteriad. The margin of this area is somewhat irregular; some of this irregularity was probably present in life, but part of it appears due to post-mortem breakage. On the ventral surface there is a series of posteriad-oriented ridges below the postero-lateral corner. The middle ridge is the most prominent. The processus

connectens is a blunted, posteriad pointing projection just lateral to the midline, dorsal to the notochord. An anteriad expanding shelf which faces postero-dorsad connects the tips of these processes with the dermal bones lying at the posterior end of the parieto-ethmoidal shield.

Lateral side of the head (Figure 2(B))

The holotype presents the left lateral side of the head. The preorbital length is the longest in tristichopterids (nearly a half of postorbital length), †*Heddeleithys* is the closest with over 40% (Jarvik 1950: Fig. 8, Snitting 2009: Fig. 4). The orbit is larger than in related tristichopterids, which have larger orbits than advanced tristichopterids (e.g. Ahlberg and Johanson 1997).

The orbit is surrounded by a supraorbito-ectal, one supraorbital, postorbital, jugal and lacrimal. The supraorbito-ectal forms the anterior border of the orbit, its dorsal extension reaches the supraorbital, its anterior extension the ectal. A small ventral process keeps the lacrimal to the ventral border of the orbit. The supraorbital forms the dorsal border of the orbit, it keeps the parietal and the intertemporal bones away from the orbit, but it does not extend posteriad beyond the posterior border of the orbit. It shows many tubules indicating that a sensory canal enters the supraorbital. Postorbital and jugal form the posterior border of the orbit. In both cases the border section is only a small part of the surrounding of the bones. The postorbital is elongated posteriorly, it has a long border with the squamosal and the intertemporal. The posterior margin contacts the supratemporal. It is closest to the narrow and elongated shape of the postorbital in †*Heddeleithys* (Jarvik 1950: Fig. 8, Snitting 2009: Fig. 4). The jugal is oval-shaped, not as square as in other tristichopterids. The lacrimal is an elongated bone, which forms the ventral border of the orbit. It overlaps ventrally the maxilla and articulates anteriorly with premaxilla, lateral rostral tectal and supraorbito-ectal. It forms the main portion of the posterior contact of the premaxilla. The infraorbital canal, which runs through the whole length of the lacrimal enters the premaxilla here.

The tectal is easily recognised with its dorsal border with two nasals and its anterior border with the premaxilla. The ventral limit of the bone is questionable. The external nasal opening and the suture with the lateral rostral can only tentatively be marked. In the parieto-ethmoid specimen UCMP 118284, the fenestrae exonarinae are also not well defined since the specimen is crushed; the right one is a mere slit running approximately antero-posteriad, whereas the left one is directed laterad. In the holotype, the anterior nasal is short compared to the elongated posterior one. The nasals are separated by a postrostral from its counterpart on the right side. In front of the postrostral lies a rostral, which separates the dorsal extensions of the premaxilla of both sides.

The dorsal margin of the lateral aspect of the head is not intact. Part of the left parietal bone is visible between the posterior nasal and intertemporal, and dorsal to the supraorbital. All these bones show rich branching tubules of the supraorbital canal. The intertemporal has a straight medial border, but is arched ventro-laterally on its contact with the postorbital; it has a short contact with the supratemporal. These anterior bones lie more or less in correct position, whereas farther behind the extrascapulae are out of position. The postparietal shield lies separately (Figure 2(A)) on the slab. There are two bones behind and above the intertemporal, the larger one is interpreted as the lateral extrascapula, because it is rich in tubules and carries an antero-posteriorly running pit line. A similar bone lies above the anterior part of the head (Figure 2(A)), it shows on the inside a cross of canals, which could correspond to the temporal canal and branching off supraoccipital commissure. On the inside of the right cleithrum lies an elongated bone with a lateral line canal following its length and continuing from the extrascapula. We interpret it here as the median extrascapula. Above the squamosal are broken bones; one larger arched piece shows tubules in the anterior part and an overlapped area in the posterior part. That element may be questionably the left posttemporal. The extratemporal is moved a little ventrally towards the squamosal and onto the opercle. It appears to be triangular and fits into the space between squamosal and opercle, a position as in †*Eusthenopteron*, bordering medially the tabular and extrascapula of the lateral skull roof.

The cheek region is formed by the postorbital, jugal, squamosal, preoperculum, quadratojugal and the posterior, deepened part of the maxilla. The squamosal is differently shaped than in closely related tristichopterids. Its postero-ventral extending portion is narrower and more elongated than in other tristichopterids. From the jugal canal branching tubules appear mainly ventral to the canal. A boomerang-shaped pit line opens postero-ventrally. The preopercle is elongated in depth and narrow, its width is only $\frac{1}{4}$ of its depth (compared with $\frac{1}{3}$ in †*Eusthenopteron foordi*); it is traversed by many tubules and pores. The quadratojugal is small and triangular where the dorso-lateral side of the triangle is 'pushed' inwards by the preopercle. A vertical pit line lies in the centre of the quadratojugal.

The premaxilla and maxilla form the upper jaw. The premaxilla is triradiate. A short medial branch meets the counterpart of the opposite side, and a broad dorsal branch reaches the anterior nasal. It borders the unpaired rostral medially and surrounds the rostral with the posterior branch. The posterior branch articulates posteriorly with the lacrimal and for a short distance with the maxilla. The arrangement of the pores indicates that the infraorbital canal runs from the premaxilla into the rostral. The premaxilla shows small marginal teeth followed medially by larger teeth. Close to the symphysis appears a large tooth, a 'pseudofang' (Snitting 2009), which is twice as

deep as the other premaxillary teeth (for additional description see below with the palate). The maxilla is very low, especially below the lacrimal and jugal, even though the posterior part of the maxilla has four times its anterior depth it appears low in the posterior cheek region. It occupies about $\frac{1}{4}$ of the cheek depth. The maxilla is shaped like that of *†E. foordi* (Jarvik 1944a: Fig. 9A) with overlap areas for the lacrimal and jugal and a dorsal extension where lacrimal and jugal meet. Like the premaxilla, the maxilla possesses small teeth on the margin and larger teeth medially.

The palate (Figure 7)

The palate of specimen UCMP 117884 is described here starting from the front (premaxilla) going backwards to the posterior end of the parasphenoid. Only the middle part of the palate is preserved, lateral and posterior bones are

missing. Two types of teeth exist at the margin of the premaxilla: an outer row of very small teeth situated right on the margin, and a row of larger teeth protruding from the inner side of this margin. The tiny marginal teeth occur uniformly along the entire length of the premaxilla; they are equally spaced and appear to project directly out of the dermal bone. Only a very few shallow depressions, perhaps qualifying as sockets, are visible. These teeth are smooth, conical and usually come to a sharp point. They are tallest where they occur between the teeth of the interior row. The tiny teeth near the symphysis are directed more or less straight downward from the jaw margin; a few are deflected laterally, but none appear to be recurved. These teeth are recurved linguad near the lateral corner of the premaxilla. There are about 5–8 of these small teeth between the larger teeth at the mouth margin.

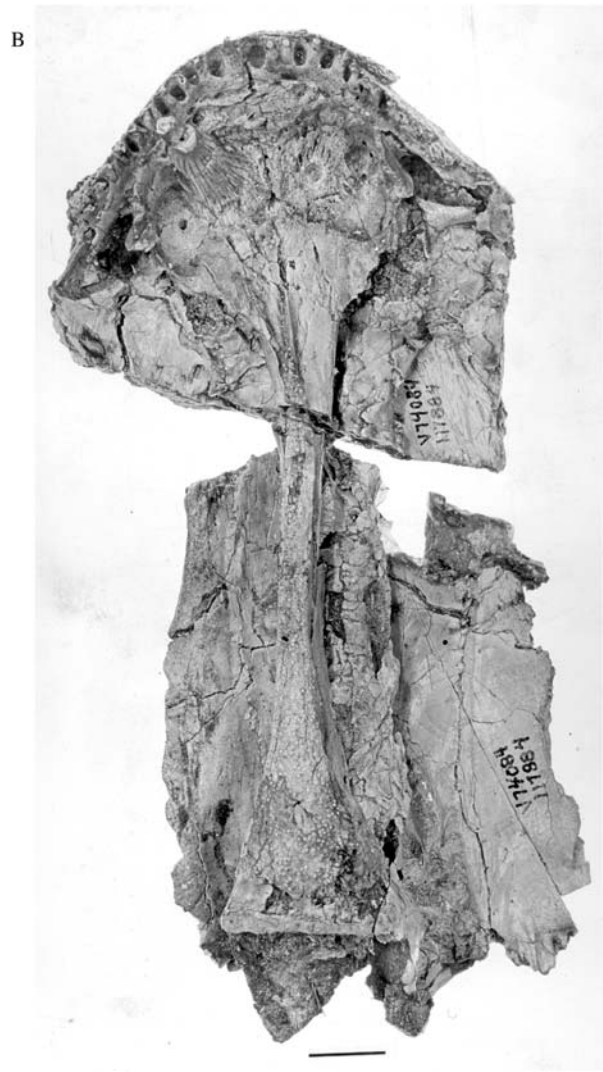
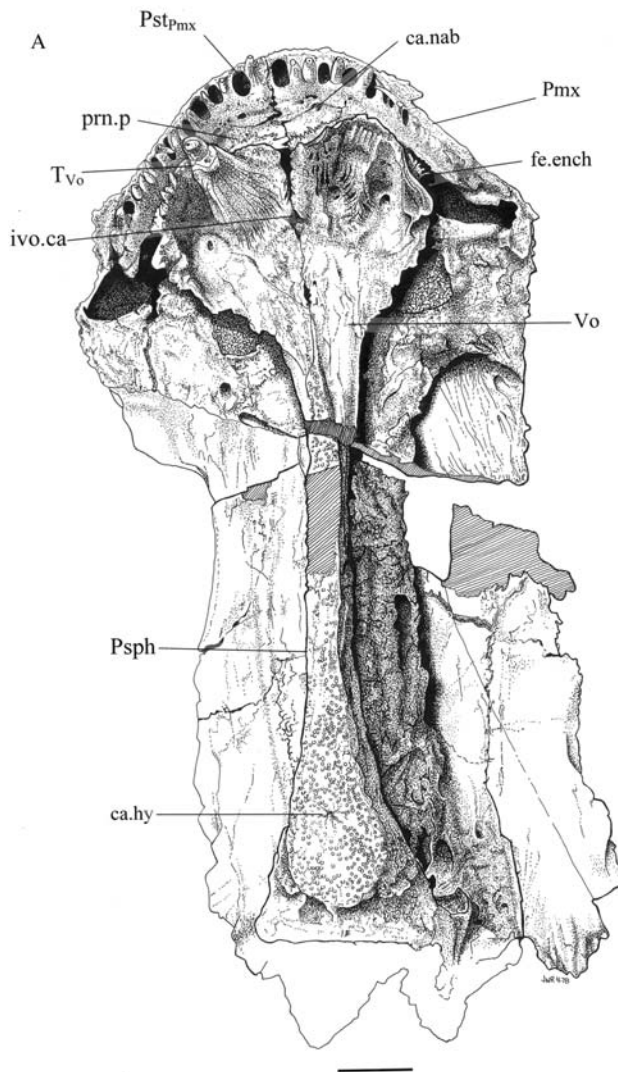


Figure 7. *†Bruehnopteron murphyi* n. sp., palate UCMP 117884. (A) drawing, (B) photograph. Scale equals 1 cm. Abbreviations: ca.nab, nasao-basal canal; ca.hy, hypophysial canal; fe.ench, fenestra endochoanalis; ivo.ca, intervomerine canal; Pmx, premaxilla; prn.p, prenasal pit; Psph, parasphenoid; Pst_{pmx}, socket for premaxillary “pseudofang”; T_{vo}, vomerine tusk; Vo, vomer.

The palatal lamina of the premaxilla slants steeply postero-dorsad at the symphysis. Two deep tooth sockets of ellipsoidal outline exist in this wall. These are the sockets for the enlarged anterior teeth of the premaxilla, the 'pseudofangs' of Snitting (2009), a character for tristichopterids above *Jarvikina*. Sockets without teeth follow postero-laterally. The sockets are more or less straight sided, but may flare slightly near their bases before the floor is reached. The floor displays a complicated enfolded pattern of bone, and is pierced in the middle by a small round hole (polyplacodont tooth structure). The teeth filling these sockets are compressed along a plane perpendicular to the mouth margin, tapering and reaching a sharp point if not broken. They bear a few striations parallel to their long axes at the base. They are recurved. The palatal lamina of the premaxilla reaches into the prenasal pit. The openings of the nasobasal canal appear antero-lateral to the pit close to the margin of the palatal lamina of the premaxilla. The vomers cover most of the lateral parts of the anterior palatal fenestra, almost reaching the palatal lamina of the premaxillary bone. The prenasal pits are shallow. The openings for the ventral branches of the nasobasal canals are situated at the antero-lateral corners of the prenasal pits.

The margin of the vomers surrounding the vomerine tusks is studded with teeth, comprising two rows. An outer row of very small, stubby teeth is poorly developed; only a few of those teeth are visible near the left lateral extent of the margin. The inner row possesses more numerous, larger teeth. The teeth are tapering, and, in contrast to the teeth of the premaxillary bone, are antero-posteriorly compressed. These teeth are somewhat blunted, and are few in number; they appear to be damaged.

The vomers meet each other in a complicated interlocking suture. The vomers are moved slightly apart as the result of crushing. A large, antero-posteriorly elongate opening leading into the intervomerine canal lies posterior to the tusks, right on the midline.

The vomers flare laterally to accommodate the tusks. There are four pits, two on each side. The right medial one is filled by a tusk, the others are empty. In this specimen, the left side apparently lost its tusk. The left medial pit looks freshly vacated; its margin encroaches on that of the lateral pit, and its floor is covered with a very complicated enfolded pattern of bone, which also extends up the sides of the vomer. A deep opening is situated in the middle of this pit. The lateral pits have flared bases and are smoother; their floors are covered with a reticulating bone pattern. All four pits are ellipsoidal with their long axis oriented approximately antero-posteriorly. The one tusk is robust, conical, tapering and striated. The point of the tusk is not preserved; its apical part is cracked and shifted antero-laterad. The tusk has a central cavity surrounded by folded dentine (polyplacodont tooth); the tusk is recurved postero-medial and is directed antero-laterad.

The vomers suture antero-laterally with the premaxilla to the anterior edge of the fenestra exochoanalis. The lateral toothed ridge of the vomer borders medially the fenestra exochoanalis. A lamina reaches from the toothed ridge into the fenestra. The opposing antero-lateral border of the fenestra exochoanalis is clearly marked. The maxilla and dermopalatine are not preserved, so the posterior half of the fenestra exochoanalis is not visible. The margin of the vomers runs in a wavy course from the fenestra exochoanalis towards their posterior processes. Here the anterior margin of dermopalatine articulates. A longer arched margin goes over to the margin of the posterior process of the vomer; here the endopterygoid sutures.

The vomers form a wide expanding shelf antero-lateral to the front end of the denticulated surface of the parasphenoid. They reach laterally far back along the denticulated area of the parasphenoid. The surface of this shelf is smooth; it reaches the vomerine tusks.

The paired vomers and the parasphenoid are attached ventrally to the ethmosphenoid along the midline of the palate.

The parasphenoid has a flat ventral surface covered with denticles, which are low, often truncated and hollow. The posterior margin of this surface is rounded and carries the hypophysial foramen. The posterior margin of the parasphenoid is straight and it flares laterally. The sides of the bone converge towards the midline anteriorly and meet at a point in the middle of the smooth shelf of the vomers. In front of it the intervomerine canal opens.

The ventral surfaces of the dermal bones of the skull roof (parieto-ethmoidal shield) are best seen on the left side; they are smooth with many tiny foramina and a few large ones. Several elongated foramina exist on the ventral dermal bone surface posterior to the posterior nasal wall. The endocranium can be seen to fuse with the dermal bones on the right side. One rather prominent antero-posteriorly directed ridge is probably a ridge below the supraorbital sensory canal.

The surface of the endocranial bones of the neurocranium is covered with hundreds of short cracks and tiny foramina. Where the neurocranium joins the dermal bones of the skull roof, the surface appears disturbed; there are numerous short and blunted ridges merging with each other. The neurocranium is only partially preserved and crushed, so no attempt is made to describe it here.

Lower jaw (Figures 2(B) and 8(A)–(C))

The left lower jaw is preserved in the holotype (Figure 2(B)) and the posterior part of a left jaw is preserved as an isolated specimen UCMP 123135 (Figure 8(A)–(C)). In both specimens the sutures between the bones of the external side are difficult to recognise. The lower jaw is of similar depth along its whole extent. The dentary occupies about

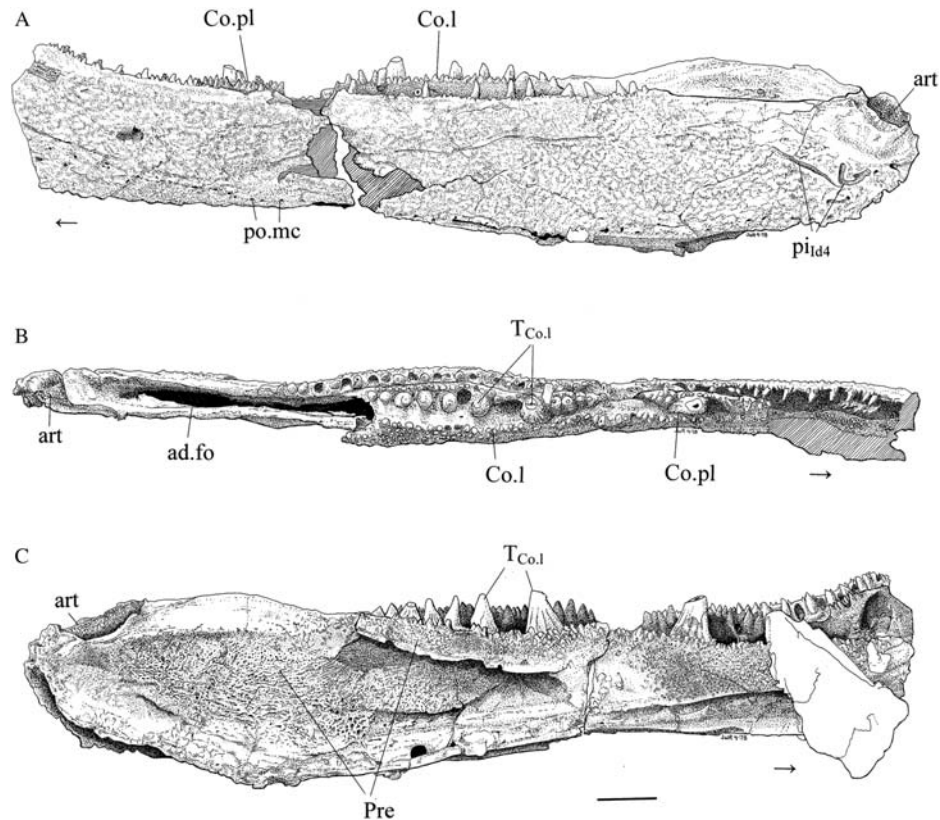


Figure 8. †*Bruehnopteron murphyi* n. sp., left lower jaw, UCMP123135. (A) Lateral view, (B) dorsal view and (C) medial view. Scale equals 1 cm. Abbreviations: ad.fo, adductor fossa; art, articular; Co.l, last coronoid; Co.pl, penultimate coronoid; pi_{id4} , pit line of infradentary 4; Pre, prearticular; $T_{Co.l}$, tusks of last coronoid; arrow points antieriad.

2/3 of the depth of the jaw along its whole length. It carries a row of very small teeth on the outer margin, followed lingually by a row of larger, pointed teeth or their sockets, respectively. The infradentaries 2 and 4 carry a pit line each (see details under *Lateral line system*). Pores of the mandibular canal appear on the ventral margin of infradentaries 4 and 3. They appear a little higher in infradentary 2, suggesting that the mandibular canal moves away from the ventral margin of the infradentaries in the two anterior infradentaries. The ornamentation of the outside of the lower jaw is identical to that on the skull roof and cheek bones.

The internal side of the lower jaw is occupied by the prearticular, which forms the whole depth in the posterior part. In front of the adductor fossa the toothed part of the prearticular starts on an elevated lamina. The lamina deepens antieriad and carries small shagreen-like teeth, which enlarge in size towards the dorsal margin of the prearticular. The holotype shows the internal side of the symphyseal area of the right dentary. The small anterior marginal tooth at the symphysis is followed by a fang of the size of the 'pseudofang' of the premaxilla. An adsymphyseal plate sits posterior to the fang. It forms an elevated pad and is covered with sockets for small teeth. There is a groove with porous bone below the pad

representing the symphyseal Meckelian cartilage. The groove is limited posteriorly by the anterior end of the prearticular, which lacks teeth in this area.

Articular, adductor fossa and coronoids lie between the dentary and prearticular. The articular at the posterior end of the lower jaw forms a simple cup-like structure for the articulation of the quadrate. The adductor fossa in front of the articular is about as long as the posterior coronoid. Two coronoids are preserved in specimen UCMP 123135; the posterior one is about twice as long as the penultimate one. The coronoids carry an outer line of small teeth, which reach the size of the inner dentary teeth on the penultimate coronoid. The penultimate coronoid carries one fang and the replacement pit of another in front of it. The last coronoid carries a row of large teeth starting with four large teeth followed by a tusk and a replacement pit; the next tooth is fang-like and is followed by a replacement pit and five teeth diminishing in size posteriad.

Opercular region (Figure 8)

The opercle and subopercle surround the cheek region posteriorly. The opercle is twice as deep as wide and is widest ventrally. The boundary between opercle and subopercle forms a wavy line as in †*E. foordi* (Jarvik 1944a).

The posterior part of the subopercle extends dorsally far above the anterior contact between opercle and subopercle. The posterior depth of the subopercle is nearly double its width. The anterior depth of the subopercle is half the depth of the opercle.

The opercular series continues as submandibular bones below the lower jaw. The most posterior submandibular is the largest and longest of the series. A straight pit line crosses the bone. Seven submandibulars lie in front of the large submandibular below the subopercle as in †*E. foordi* (Jarvik 1944a). The sixth submandibular carries a short pitline. The left gular is the lowest bone preserved in the specimen extending from the last submandibular bone to in front of the first submandibular bone. The anterior part in front of the first submandibula is smooth without the tubercles, instead it shows some ridges. This may represent the overlap area for the median gular. We could not find any pit line on the lateral gular.

Lateral line system

The course of the sensory canals is indicated by the openings of the outgoing tubules (pores) and by the tubules themselves in the KUVP specimen. The tubules indicate a richly branching lateral line system. The pores themselves are about 0.1 to 0.2 mm in diameter; they are not aligned in rows, but neither are they scattered at random. They are closely distributed around the sensory canals. They usually open between tubercles, but may open out of the side of a tubercle. The pores may face straight up, or they may be at an angle to the surface; occasionally they may open nearly parallel to the surface (appearing as tubules).

Temporal canal and occipital commissure

The temporal canal runs antero-posteriad through the middle of the tabular and supratemporal of the postparietal shield (Figure 2(A)). It enters the tabular from the lateral extrascapula. The left lateral extrascapula shows a rich branching of tubules indicating a branching of the supraoccipital commissure from the temporal sensory canal. The supraoccipital commissure has less branching tubules in the median extrascapula as indicated by less pores. The right lateral extrascapula presents the inside with branching canals, temporal canal and branch of the supraoccipital commissure. The temporal canal enters anteriorly the intertemporal bone where it splits into supraorbital and infraorbital canals. The course of pores indicates the ventral course of the infraorbital canal. The rich branching of tubules in the supraorbital bone (Figure 2(B)) indicates that a branch enters the bone from the intertemporal.

Supraorbital canal

The supraorbital canal runs anteriorly from the postero-lateral corner of the parieto-ethmoidal shield, the intertemporal. The supraorbital canal passes through the lateral part of the parietal, before it enters the two nasal bones and continues into the premaxilla, where it meets the infraorbital canal (Figure 2(B)).

Infraorbital canal

The infraorbital canal branches off within the intertemporal bone. The pores of this branch open close to the margin of the shield. The infraorbital canal runs through the anterior part of the postorbital, the growth centre, into the jugal (Figure 2(B)). In the jugal the horizontal part of the infraorbital canal is best visible; it continues posteriad as jugal canal. The infraorbital canal runs in the lower part of jugal, lacrimal and premaxilla. It passes from the lacrimal into the premaxilla without passing through the lateral rostral. The course of the infraorbital canal is visible on the anterior part on the snout just above the tooth bearing margin. The pores here are slightly larger than those of the main part of the canal.

Preopercular and jugal canal

The jugal canal branches off from the infraorbital canal in the centre of the lower part of the jugal. It enters the squamosal above the antero-ventral corner of the squamosal and runs in a weak bow through the squamosal to enter the preopercle in its dorsal part (Figure 2(B)). In the squamosal, it seems as if most branching tubules are directed ventrally. The sensory canal continues in the middle of the preopercle and enters the quadratojugal ventrally.

Mandibular canal

The mandibular canal is the continuation of the preopercular canal in the lower jaw. In the holotype (Figure 2(B)), rich branching is visible in infradentaries 4 and 2. Specimen UCMP 123135 shows a row of pores along the ventral margin that indicates a course of the mandibular canal in the ventral part of the lower jaw.

Pit lines

Pit lines are sparsely developed. An elongated, antero-posterior running pit-line can be seen medial of the break on the left lateral extrascapula. The postparietal pitline is developed as an arched line on the tabulars only (Figure 3). Nothing is seen on the postparietals. The parietal pitlines are short; they reach from the middle lateral side of the parietal in an arch to the level of the pineal foramen. They are farther posterior than in †*Eusthenopteron* as is the pineal foramen. A boomerang-shaped pit line opening

postero-ventrally is visible in the lower part of the squamosal, and a straight, vertical pit line occurs on the quadratojugal (Figure 2(B)). Two pit lines are present on the infradentary series of the holotype (Figure 2(B)). One on infradentary 4 runs in an arch from the ventral margin of the bone dorso-anteriad; the second on infradentary 2 forms a right angle between lower posterior part and the horizontal dorso-anterior part. Specimen UCMP 123135 has two pit lines on infradentary 4, one boomerang-shaped and in front of it another running oblique from postero-ventral to antero-dorsal. Pit lines were observed on submandibular bones 6 and 7, but not on the gular.

Shouldergirdle (Figures 2(A),(B) and 9(A),(B))

The right cleithrum lies above the anterior part of the head of the holotype (Figures 2(B) and 9(A)); it shows the internal face of the cleithrum with the scapulocoracoid. The cleithrum has the typical shape of a tristichopterid or osteolepiform cleithrum (Jarvik 1944b [*†Eusthenopteron*], 1985 [*†Spodichthys*]; Gross 1956 [*†Latvius*]; Andrews and Westoll 1970 [*†Eusthenopteron*]) with a strongly developed process that overlaps the dorsal part of the clavicle. The process is developed on the left cleithrum of *†Bruehnopteron*, whereas it is lacking on the right cleithrum. The lower part of the left cleithrum is preserved on the right margin of the plate containing the holotype (Figure 2(A)). It has the typical scoop-like shape with the overlap area for the clavicle anteriorly. The overlap area for the clavicle is bordered dorsally by a short process at the anterior margin of the cleithrum.

The scapulocoracoid attaches in three areas to the cleithrum as in *†Eusthenopteron* and *†Spodichthys* (Jarvik 1944b: Fig. 4D, 1985, Fig. 32D, E; Andrews and Westoll 1970: Figs. 1c, 3f–j; Snitting 2008b, Fig. 9B), the anterior,

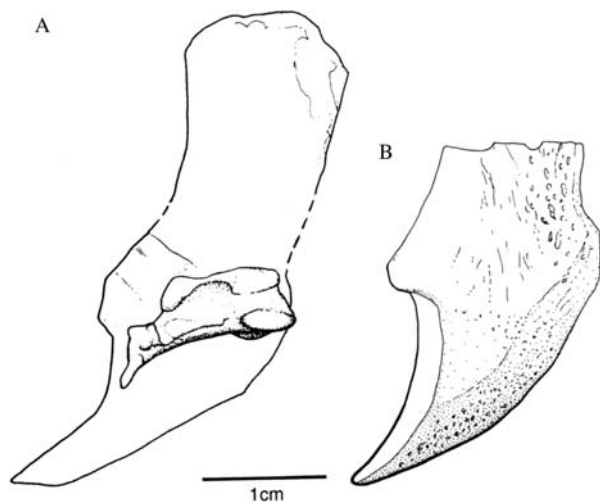


Figure 9. Cleithra of holotype of *†Bruehnopteron murphyi* n. sp., KUVF 94040, (A) internal view of right cleithrum, (B) external view of ventral part of left cleithrum. Scale equals 1 cm.

dorsal and posterior attaching processes of the scapulocoracoid are visible. The scapulocoracoid shows three buttresses on its medial side, called infraglenoid, glenoid and supraglenoid buttresses in Jarvik (1985). The supraglenoid buttress lies directly dorsal to the glenoid buttress, not anterior to the glenoid buttress as in *†Spodichthys* (Jarvik 1985: Fig. 32F).

Comparison, discussion and conclusions

The content of the family *†Tristichopteridae* Cope 1889 (= *†Eusthenopteridae* Berg 1940) has not much changed since the publication of the *Osnovy* (Vorobjeva and Obruchev 1964), which included the genera *†Tristichopterus*, *†Eusthenopteron*, *†Eusthenodon* and *†Platycephalichthys*. Subsequent additions were *†Hyneria* by Thomson (1968), *†Jarvikina* by Vorobjeva (1977), *†Notorhizodon* by Young et al. (1992), *†Mandageria* by Johanson and Ahlberg (1997), *†Cabonnichthys* by Ahlberg and Johanson (1997) and *†Langlieria* by Clément et al. (2009).

In addition, there is little difference between published phylogenetic relationship schemes of the *†Tristichopteridae* by Johanson and Ahlberg (1997), Ahlberg and Johanson (1998) (see Young 2008), Snitting (2008b) and Clément et al. (2009). After Snitting (2008a), *†Platycephalichthys* must be divided and only the species with round scales belongs to the *†Tristichopteridae*. *†Hyneria* is too not completely known and has been left out of phylogenetic analyses. The species *†E. dalglesiensis* has been elevated to its own genus, *†Heddeleithys* (Snitting 2009). Most recently the poorly preserved genus *†Langlieria* has been added to the advanced tristichopterids *†Cabonnichthys*, *†Mandageria* and *†Eusthenodon* (Clément et al. 2009). Thus, the concept of the family and the interrelationships of its genera have been very stable and have changed only by addition of genera over the years. Jarvik (1985) described the osteolepiform genus *†Spodichthys* from the Upper Devonian of Greenland. This genus is basal to all tristichopterids in the phylogenetic scheme of Snitting (2008b), but the extratemporal of *†Spodichthys* is unknown. There is a short attachment area at the postero-lateral corner of the tabular for the extratemporal, nevertheless it cannot be demonstrated that the extratemporal reaches into the postspiracular area, which is the defining character of *Tristichopteridae* after the above-cited phylogenetic analyses. The extratemporal occupies nearly the posterior half of the lateral side of the tabular in *†Eusthenopteron* and *†Heddeleithys*, whereas it just reaches the tabular or is eliminated from it in advanced tristichopterids.

The postorbital and jugal participate in the margin of the orbit in *†Bruehnopteron* n. gen. as in the basal tristichopterids *†Tristichopterus*, *†Eusthenopteron*, *†Jarvikina* and *†Heddeleithys* (Figure 10), whereas the postorbital or both bones are excluded from the orbit in the advanced tristichopterids (*†Cabonnichthys*, *†Mandageria*,

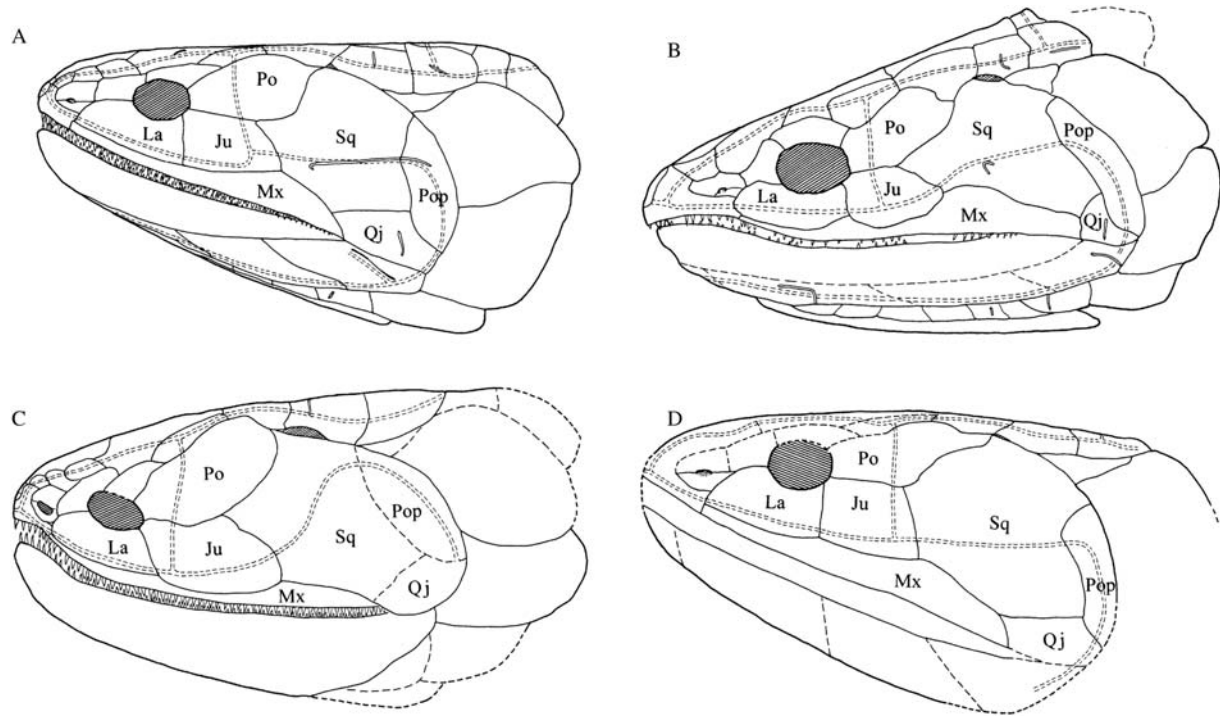


Figure 10. Lateral view of basal tristichopterids. (A) †*Eusthenopteron foordi* Whiteaves 1881 (after Jarvik 1944a, changed after specimens MHN 06-2065 and 06-1494), (B) †*Bruehnopteron murphyi* n. gen. n. sp., (C) †*Jarvikina wenjukowi* (Rohon 1889) (after Vorobjeva 1977, changed), (D) †*Heddeleithys dalglesiensis* (Anderson 1859) (after Jarvik 1950 and Snitting 2009). Abbreviations: Ju, jugal; La, lacrimal; Mx, maxilla; Po, postorbital; Pop, preoperculum; Qj, quadratojugal; Sq, squamosal.

†*Eusthenodon*). The infraorbital canal passes directly from the lacrimal into the premaxilla in †*Bruehnopteron* without passing through the lateral rostral as described above. The same situation can be found in other tristichopterids even in †*E. foordi* (see juvenile †*E. foordi* in Schultze 1984 and in contrast to Jarvik 1944a) as the examination of specimens MHN 06-1494 and 06-2065 of the Miguasha museum demonstrates. As the Red Hill species was earlier considered a species of †*Eusthenopteron*, it fits in its character set with the basal tristichopterids (†*Tristichopterus* to †*Heddeleithys*) in the participation of postorbital and jugal at the posterior orbital margin, the posterior process of the supraorbital not extending beyond the posterior orbit margin, the lack of accessory vomers, the presence of marginal teeth on the anterior part of the dentary and on coronoids. The condition of the posterior coronoid (two fangs and much longer than the penultimate coronoid) characterises †*Bruehnopteron* as more advanced than †*Tristichopterus*, and the position of the pineal foramen well behind the orbits is more advanced than †*Eusthenopteron*. The possession of fangs on the anterior dentary and on the premaxilla places it above †*Jarvikina*, and the lack of cutting edges on fangs and the lack of a kite-shaped pineal area place it below the phylogenetic position of †*Heddeleithys* (Snitting 2008a).),

Specimens of †*Heddeleithys dalglesiensis* (Anderson 1859) are poorly preserved. Jarvik (1950: †*E. dalglesiensis*) and Snitting (2009: †*H. dalglesiensis*) redescribed the holotype of †*Diplopterus dalglesiensis* Anderson 1859. Snitting (2009) used computed tomography to add internal structures. †*Heddeleithys* is separated from species of †*Eusthenopteron* perhaps by the overall narrowness of the whole head, though the difference is very small and the holotype is crushed laterally (Jarvik 1950, plate 10: Fig. 3). The relatively shorter length of the postorbital division separates †*H. dalglesiensis* (Figure 10(D)) from †*Jarvikina wenjukowi*, †*B. murphyi*, †*E. cf. traquairi*, †*E. traquairi* and †*Platycephalichthys*. The posterior position of the pineal area distinguishes †*Heddeleithys* from species of †*Eusthenopteron*. The possession of fangs on the anterior dentary and on the premaxilla, cutting edges on fangs and a kite-shaped pineal area separates †*Heddeleithys* from †*Jarvikina*.

Vorobjeva (1977) separated †*E. wenjukowi* from other species of †*Eusthenopteron* as a new genus, †*Jarvikina*. Of the 19 characters listed as diagnostic for this genus, only about half are actually visible in photographs or drawings; and of these, only three are different from the condition in †*E. foordi*. Furthermore, two of these (scales widely overlapping and scales with network ornamentation) are of dubious value. That the scales figured by Vorobjeva

actually belong to †*J. wenjukowi* is not certain either (they appear to be disarticulated). A number of diagnostic characters mentioned concern the lengths of parts in comparison with other parts. Without articulated material, it is difficult to understand how these ratios were arrived at. The endopterygoid figured by Vorobjeva (1977, plate 12: Fig. 3) looks somewhat different to that of †*E. foordi*. However, her specimen appears to be broken, and it seems possible that the processus ascendens (pac) and the notch for the trigeminal nerve (n. V) were actually farther forward, where a piece of the bone seems to be missing. Zupinš (2008) described an additional species of †*Eusthenopteron*, †*E. kurshi*, which looks similar to †*J. wenjukowi*. Both species possess a posteriorly rounded postorbital and a short preorbital region. Squamosal, preopercle and quadratojugal are fused in †*E. kurshi*; Vorobjeva (1977) reconstructed the boundaries between the three bones in †*J. wenjukowi*.

The only character that clearly differentiates †*E. foordi* from †*J. wenjukowi* is the position of the pineal opening. In †*E. foordi*, the pineal opening is at a similar level to the centre of radiation of the parietal bones and posterior to the orbits. In †*J. wenjukowi*, the centre of radiation of the parietal bones is anterior to the pineal area and the pineal foramen lies far posterior to the posterior margin of the orbits.

†*Bruehnopteron* corresponds in the position of the pineal foramen with †*Jarvikina*. The parietal pit-line on each side is located anterior to the pineal foramen (vs. †*E. foordi* and †*E. saevesoederberghi*), a position as in advanced tristichopterids (see Young 2008). The pores of the sensory canals do not closely approach the pineal opening (vs. †*E. foordi* and †*E. saevesoederberghi*). In addition, the possession of fangs ('pseudofangs') near the symphysis of the dentaries and of the premaxillae places the genus above †*Jarvikina*, whereas the lack of cutting edges on fangs and lack of a kite-shaped pineal area places †*Bruehnopteron* below †*Heddeleithys* in the phylogenetic scheme of Snitting (2008a).

Besides these phylogenetically important characters, there are smaller, less important differences to distinguish †*B. murphyi* from species of †*Eusthenopteron*, †*Jarvikina* and †*Heddeleithys*. The genus is uniquely characterised by the elongated shape of the lacrimal, the oval shape of the jugal, a postero-ventral elongated squamosal, a deep and narrow preopercle, a small triangular quadratojugal and the longest preorbital region of all tristichopterids.

†*Bruehnopteron* is interpreted here as a 'moderately derived' tristichopterid in the sense of Snitting (2009, p. 282) in contrast to Swartz (2012) who places another sarcopterygian specimen of the same locality at the base of the Elpistostegalia. Our interpretation supports the conclusion by Reed (1979) based on intensive comparison with †*Eusthenopteron* species and closely related genera.

Acknowledgements

The basis of this paper was part of Reed's doctoral thesis at the University of California, Berkeley. The excavations in 1974 and 1975 were supported by the University of California, Berkeley. Reed was the guest at the Svenska Naturhistoriska Riksmuseet, Stockholm, in 1977–1978. The stay was financed by the American Scandinavian Foundation and the University of California. The excavations in 1981 and 1983 were supported by the Division of Vertebrate Paleontology, Museum of Natural History, University of Kansas; the excavation of 1987 was supported by National Geographic grant 3516-87 to Schultze. The senior author is thankful to O. Bonner, former preparator at the Division of Vertebrate Paleontology, the former graduate students Dr J. Chorn, Dr M. Gottfried and Dr J. McAllister and the German helping hands, P. Brühn and E. Thomas, for their hard work in the field. Dr M. Murphy gave us the opportunity to use the field facilities of the geological field camp of University of California, Riverside in the Roberts Mountains. The authors also thank L. Berner (Museum für Naturkunde in Berlin, Germany) for his careful preparation of specimen KUVF 94040. The senior author thanks Pat Holroyd (UCMP) and Brian Swartz for help in the vertebrate paleontology collection during the visit in 2007. Figures were drawn by J.W. Reed (Figures 4–8) and Mr J.-P. Mendau, Berlin (Figures 2(B), 3, 9(B) and 10). F. Charest (MNHM) kindly supplied pictures of the snout of †*E. foordi* specimens in the collection of the Miguasha museum (MNHM 06-505, 06-1494, 06-2065). The authors also thank P. Ahlberg and G. Young for their helpful comments and the correction of the English.

Note

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Addendum

Swartz (2012) created a new genus and species for a large piscine sarcopterygian (*Tinirau clackae*) of the Red Hill locality in Nevada. The reconstruction of the lateral side of the skull is so different that it may justify the assignment of *Tinirau* to a different taxon (Elpistostegalia) than *Bruehnopteron* (Tristichopteridae). *Tinirau* has a pointed skull with a long postorbital length (preorbital in postorbital length 26% compared to 48% in *Bruehnopteron*). In contrast to *Bruehnopteron*, the jugal has an elongate posterior process, the cheek bones are fused to a dermal plate, the maxilla is long and narrow, and the operculum is less deep compared to the suboperculum in *Tinirau*. The shape of postorbital and supraorbital are different at least in the reconstruction, and there are less bones of different shape in the preorbital region of *Tinirau*. The large specimen was not included in Reed's PhD thesis, whereas the small specimens UCMP 117884 (Fig. (5) = Swartz 2012 Fig. 3A-I, Fig. (7) = Swartz 2012 Fig. S2) and UCMP 118283 (Fig. (8) = Swartz 2012 Fig. S5) were and are here considered as belonging to a tristichopterid, *Bruehnopteron*.

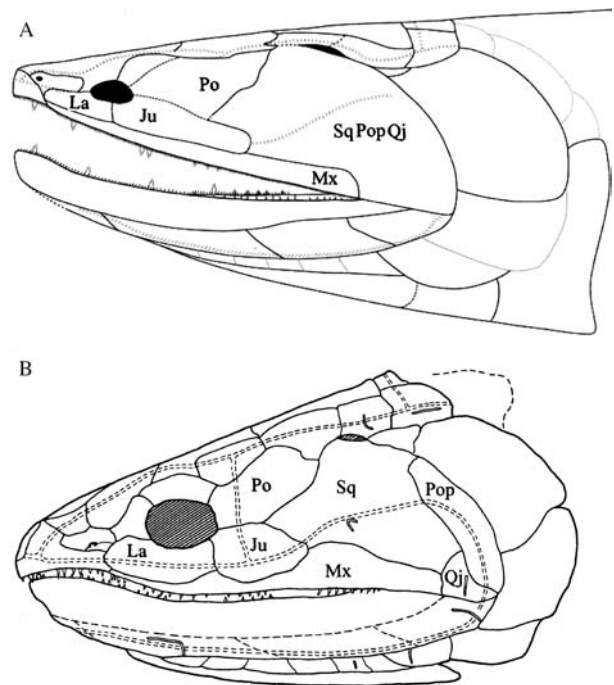


Figure 11. Comparison of head in lateral view of (A) †*Tinirau clackae* Swartz, 2012 with (B) †*Bruehnopteron murphyi* n. gen. n. sp., both from the same locality, Red Hill, Northern Simpson Range, Nevada. Abbreviations: Ju, jugal; La, lacrimal; Mx, maxilla; Po, postorbital; Pop, preoperculum; Qj, quadratojugal; Sq, squamosal; SqPopQj, fused cheekbone. (A) courtesy of Brian Swartz.

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