# A NEW TRISTICHOPTERID (PISCES, SARCOPTERYGII) FROM THE DEVONIAN OF LATVIA 

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#### Abstract

A new species of tristichopterid sarcopterygians, Eusthenopteron kurshi, sp. nov., the earliest representative of the family reported to this date from the territory known as the Main Devonian Field, is described from the well-known fossil locality of Latvia, the Lode clay quarry (Upper Givetian/Lower Frasnian). One complete skeleton and several disarticulated bone elements of the head and shoulder girdle have been found. The material reveals some morphologic features like a relatively short parietal shield in the cranial roof and rather asymmetric caudal fin. Characteristic features for the species are a front end of the squamosal extending comparatively far anteriorly and opercular being twice as high as the subopercular.


Key words: vertebrates, Givetian, Frasnian, morphology.

## INTRODUCTION

Since the early 1970s, the Lode clay quarry (Cēsis District, Latvia) has proved to be a rich Devonian fossil fish locality of world-wide importance. It is well known among palaeoichthyologists due to exceptionally well-preserved fossils of various groups of fishes that have been found there. In contrast to other fossil fish localities in Latvia where mainly fragmentary or disarticulated bones can be found, complete skeletons of a placoderm Asterolepis ornata, sarcopterygians Laccognathus panderi, recently claimed to be a new species Laccognathus grossi (Vorobyeva, 2006), and Panderichthys rhombolepis have been found at the Lode clay quarry during the early years of excavations (Lyarskaya and Mark-Kurik, 1972; Vorobyeva, 1980). Finds from this locality have already yielded a lot of data adding new knowledge to our understanding of Devonian fish morphology, diversity and environment. Comprehensive publications dealing with sedimentological and preservational aspects of the fish remain accumulations within clay and silt beds of the Lode quarry have been published quite recently (Kuršs et al., 1998; 1999). Discovery of fossils of juvenile individuals of placoderms Asterolepis ornata (Upeniece and Upenieks, 1992), acanthodians Lodeacanthus gaujicus (Upeniece, 1996) and sarcopterygians Strunius and Latvius are of great scientific value (Upeniece, 1995). Lately yet another new sarcopterygian species-a coelacanth Miguashaia grossi has been reported from the quarry (Forey et al., 2000). All these finds have allowed reconstructing a whole taphocenosis represented by the fossil remains collected from the quarry over the years (Upeniece, 2001). Altogether 15 fossil vertebrate species (including the one described
here), several forms of invertebrates (arthropods) and plants are known from this locality by now.

The new material described here is the first record of tristichopterid remains from as early as the Gauja Regional Stage (Lower Frasnian). It is officially accepted that the Lode Formation is Early Frasnian by its age. According to opinion of some authors (Esin et al., 2000; Forey et al., 2000) the rocks where the fossils were found are attributed even to the Middle Devonian (Upper Givetian). In any case Eusthenopteron kurshi sp. nov. appears to be the earliest tristichopterid reported from the north western part of the East European platform (also referred to as the Main Devonian Field) sharing some similarities to another early tristichopterid Tristochopterus alatus (Givetian, Scotland).

## MATERIALS AND METHODS

All the specimens attributed to the new species come from a single locality, the Lode clay quarry. The material was collected in 1993 during excavations by the Natural History Museum of Latvia and in 1996 and 1997 individually by the author. All of the specimens are in the collections of the Natural History Museum of Latvia.

The preparation work was done mechanically using a mounted needle to remove the excess of the rock to uncover the fossils as far as considered safe for the preservation of specimens. For improving the contrast to show the details of structures the bones were covered in magnesium oxide before taking photographs.

To make the results comparable to previous studies on related material, the same scheme for taking measurements was chosen. Proportions of the head bones were calculated on the basis of the suggestions given by E. Jarvik (Jarvik, 1948) and for the body ratios using the approaches of H.-P. Schultze (Schultze, 1984).

The abbreviations for anatomical structures used in figures are as follows (in the order of appearance):

P - parasphenoideum; Vo - vomer; chn - choana; fo. ap. apical fossa; Acltr - anocleithrum; Cl - clavicle; Cltr cleithrum; Ext. 1. - lateral extrascapular; Fr-et - parietal (frontoethmoidal) shield; Gu - gular; Ju - jugal; Lac - lacrimal; Mand - lower jaw; Mx - maxillary; Op - opercular; Po - postorbital; Ppa - postparietal shield; Psp. postspiracular; Pt - posttemporal; Sbm - submandibulars; Sbm-branch - submandibulo-branchiostegal; Scl - sclerotic ring; Scltr - supracleithrum; So. p. - posterior supraorbital; Sop - subopercular; $\mathrm{Sq}+\mathrm{Pop}+\mathrm{Qj}$ - squamosal, preopercular and quadratojugal complex; na - nasal opening; Co coronoids; De - dentary; Mek - Meckelian bone; Praeart prearticular; Pspl - parasymphysial dental plate; art - articular surface; fo.add. - adductor fossa; fo.praeco precoronoidal fossa; sy - symphysis.

Material. LDM G 291/23 complete skeleton (includes also a counterpart of the posterior part of the body); LDM G 291/13, lower jaw; LDM G 291/33, anocleithrum; LDM G 291/34, fragmentary subopercular; LDM G 291/58, ethmoideum; LDM G 291/59, lower jaw and fragmentary squamosal; LDM G 291/60, maxillary; LDM G 291/61, fragmentary lower jaw (the articular part of the jaw); LDM G 291/62, cleithrum with scapulocoracoideum; LDM G 291/63, postspiracular; LDM G 291/64, posterior supraorbital; LDM G 291/65, opercular; LDM G 291/99, parietal (frontoethmoidal) shield.

## RESULTS

Order Osteolepiformes Berg, 1937
Family Tristichopteridae Cope, 1889
Genus Eusthenopteron Whiteaves, 1881
Eusthenopteron kurshi, sp. nov.
(Figs. 1-5).

Etymology. Named in honour of Prof. Visvaldis Kuršs (1928-2000), Latvian geologist who carried out extensive sedimentological studies of the Devonian rocks in the Baltic region, research that also includes detailed reconstruction of the palaeobasin conditions for the area where the Lode quarry is located.

Diagnosis. Fishes of moderate size-up to 55 cm . Vomers are tightly fused; their anteromedial corners extend forwards thus forming a slightly convex margin of the vomer pair. Parietal/postparietal shield ratio is 1.57 . Front end of the squamosal extending anteriorly further than presumable line between the ethmoideum and the otico-occipital division of the neurocranium. Opercular is twice as high as the subopercular. Caudal fin is asymmetrical; epichordal lobe forming approximately one third of the total height. All the teeth on the lateral edge of coronoids are equal in size.

Holotype. Complete skeleton (LDM G 291/23); Lode clay quarry, Latvia; Lode Formation, Lower Frasnian, Upper Devonian.

General structure. The type specimen (Fig. 1) being the only complete specimen gives notion on the general proportions of the body of Eusthenopteron kurshi. Total body length of the individual preserved in the specimen LDM G 291/23 reaches 36.6 cm . A single opercular (LDM G 291/65) is reasonably larger than the one in the holotype suggesting that individuals of $E$. kurshi might have reached at least some 55 cm in length.

Following the scheme for body proportion measurements used by H.-P. Schultze (Schultze, 1984) E. kurshi is compared to Eusthenopteron foordi Whiteaves, 1881 (Frasnian, Canada) which yields comparable data (Table 1). The results indicate a more posterior position of the dorsal and the pelvic fins in E. kurshi if compared to the fins in E. foordi.

Another character also discussed in more detail below concerns the proportions of the caudal fin. It has been noticed that in Tristichopterus alatus Egerton, 1861 (Givetian, Scotland) the vertical asymmetry of the caudal fin is greater than it is in E. foordi (Traquair, 1890). The upper (epichordal) lobe in the tail fin is $1 / 3$ of the total height of the fin in T. alatus, while in E. foordi it forms 3/7. In this aspect E. kurshi is much more similar to the early and primitive T. alatus showing the same caudal fin proportion.


Fig. 1. Eusthenopteron kurshi sp. nov., complete skeleton, holotype (LDM G 291/23). Scale bar: 1 cm .

BODY PROPORTIONS OF EUSTHENOPTERON FOORDI (ADAPTED FROM SCHULTZE, 1984) AND EUSTHENOPTERON KURSHI SP. NOV.

| Specimen\Ratio | Op-1.D/ <br> st. 1. | Op-2.D/ <br> st. 1. | Op-Cd/ <br> st.1. | Op-K/ <br> st. 1. | Op-Pelv/ <br> st. 1. | Op-An/ <br> st. 1. | Op-Cv/ <br> st. 1. | abs. 1./ <br> st. 1. |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| E. foordi (MHNM6-128) | 30.2 | 46.4 | 61.3 | 77.3 | 37.6 | 49.7 | 60.3 |  |
| E. foordi (MHNM6-128) | 29.6 | 46.2 | 59.7 | 78.8 | 39.6 | 52.9 | 61.3 | 104.6 |
| E. foordi (CCHp) | 36.1 | 52.6 | 67.1 | 82.8 | 45.4 | 60.5 | 69.5 | - |
| E. foordi (CCHcp) | 28.9 | 46.1 | 61.2 | 76.7 | 36.0 | 50.2 | 62.3 | - |
| Mean for E. foordi | 31.2 | 47.8 | 62.3 | 78.9 | 39.7 | 53,4 | 63.4 | 102.9 |
| E. kurshi (LDM G 291/23) | 42.6 | 56.5 | 67.6 | 75 | 50 | 54.5 | 63.7 | 108.9 |
| Difference if comparing to the | 36.5 | 18.2 | 8.5 | 4.9 | 25.9 | 2.1 | 0.5 | 5.8 |
| mean value (in \%) |  |  |  |  |  |  |  |  |

Neurocranium. Specimen LDM G 291/58 (Fig. 2) gives us some insight into the structure of the ethmoidal portion of the neurocranium of $E$. kurshi. Preserved is the anterior part with vomeral bones and the parasphenoideum attached. On the ventral surface of ethmoideum near the anterior end of the parasphenoideum on either side of it there are distinct elongated areas where medial ends of palatoquadrate were attached stretching above the horizontal lamina of the vomeral bones. Lateral sutures for the contact with palatoquadrate are invisible as these areas of the specimen are poorly preserved.

Large oval shaped choanas leading to the nasal cavity are situated anterolaterally to the ethmoid-palatoquadrate suture. Anterior ends of the openings are medially orientated. Thus, they appear to differ from Eusthenopteron obruchevi (Воробьева, 1977) (Amata Regional Stage) which has rather round choanas.

Choana was encircled by the lateral edges of the vomer, anterior end of the palatoquadrate and maxillary and the posterior end of the premaxillary. Both vomeral bones are tightly fused, their anteromedial corners extend forwards thus forming a slightly convex margin of the vomer pair which is not the case in E. foordi and Eusthenopteron saeve- soederberghi Jarvik, 1937 (Pḷaviñas Regional Stage) displaying shallow incisure along the front end of the suture
of both bones. Each vomer carries a fang in the middle of the plate and a row of marginal smaller teeth along its front edge. In E. foordi there are two rows of marginal teeth with the front-row teeth smaller than these of the second row. The state of these features is unknown in most other species of Eusthenopteron and in T. alatus. There is a short and shallow apical fossa between the premaxillaries and the vomers.

Cranial roof. The elements of the cranial roof in E. kurshi are tightly fused. Only the pore openings of the supraorbital sensory canal allows judging the position of the bones of nasal series. Out of the three specimens representing the parietal shield only LDM G 291/99 shows a pineal opening (=parietal foramen). It is situated opposite the hind end of the posterior supraorbital, slightly behind the level of the orbit. As observed in specimens LDM G 291/23 and LDM G 291/64 the posterior supraorbital is loosely attached to the rest of the parietal shield. A single nasal opening lies on either side of the parietal shield close to its ventral margin, thus being practically invisible if looking at the head from above. Premaxillaries carry a row of small teeth equal in size; only the teeth on its medial flank are slightly larger than the others.

Also, the bones of the postparietal shield are fused and the actual suture lines are hidden. Only the laterally extending


Fig. 2. Eusthenopteron kurshi sp. nov. Ethmoideum: A, specimen LDM G 291/58 in ventral view; B, anterior part of the same specimen. Scale bar: 1 cm .
flank of the postparietal is marked by the characteristic pit line on its surface. If compared to the other tristichopterid species found in the north western part of the East European platform represented by comparable material E. kurshi differs in several aspects. The postorbital in E. kurshi overlaps anterior corners of supratemporal to a lesser extent than in Eusthenopteron obruchevi Vorobyeva, 1977 (Воробьева и Лярская, 1968; Pl XI, Fig. 3).

The parietal/postparietal length ratio for E. kurshi is 1.57. This ratio, considered as a significant generic character for a long time (Jarvik, 1948), is calculated on the basis of the only specimen complete enough to provide the measurements for this character. The two blocks of the cranial roof are held together only by soft tissues without any additional firm contact between the parietal and postparietal shield (Zupiņš, 2003). Consequently, they tend to detach rather easily and early in the process of disintegration of sarcopterygian bodies. As a result, two blocks from the same individual are found together extremely rarely, thus restricting the amount of data available for measurements of that ratio.

The posterior end of the cranial roof is formed by medial and two lateral extrascapular bones. The medial extrascapular is poorly preserved in our material. The lateral extrascapular does not differ much from that of E. foordi being in general triangular in its shape with a rounded posterior corner.

Character of the ornamentation of dermal bones of E. kurshi fits well in line with that observed in Tristichopterus and other species of Eusthenopteron. It is formed of isolated rounded tubercles frequently fused together in rows, especially along the margins of bones. A characteristic feature of E. kurshi ornamentation is tubercles that are somewhat less pointed than in other species and are relatively larger.

Cheek plate comprises lacrimal, jugal, postorbital, squamosal, preopercular, maxillary and quadratojugal bones (Fig. 3). During the stage of compaction of sediments embedding the fish remains of the specimen LDM G 291/23, the body of the fish has been laterally flattened. As a result
the dermopalatine bones abutting the ventral edge of the dermal plate have badly smashed the lacrimal. Only its posterodorsal corner is preserved. Also, the upper margin of the front end of the maxillary is exposed showing the areas overlapped by the lacrimal and jugal. The posterior portion of the maxilla is higher than its front half and dorsally overlaps the squamosal and quadratojugal. The oblique posterodorsal edge of the jugal connects the squamosal by overlapping its ventral front end. The anterior and dorsal margin of the jugal borders the lacrimal and postorbital respectively. Apparently the ventral and posterior margin of the orbit is mainly formed by the lacrimal and postorbital allowing just the most anterodorsal corner of jugal to reach the orbital opening. The anterodorsal corner of postorbital contacts the posterior supraorbital. The hind portion of the postorbital is rather rounded and fits the loop formed by supratemporal and squamosal. A unique feature of E. kurshi is the triangular front end of the squamosal extending anteriorly further than it is in other species represented by comparable material. In E. foordi the front tip of the squamosal lies in line with the contact between parietal and post-parietal-the intracranial joint (connection between the ethmoideum and the otico-occipital division of the neurocranium) whereas in LDM G 291/23 significantly exceeds the line. There are some further differences comparing the new species with some other early tristichopterids. In Eusthenopteron ? dalgleisiensis the posterior extension of the postorbital stretches as far as the spiracular opening nearly separating the squamosal from supratemporal (Jarvik, 1950, Fig. 8). In T. alatus the jugal covers approximately a quarter of the whole orbital margin (Traquair, 1875; Figs. 1, 11), which is more than in E. kurshi.

The squamosal, preopercular and quadratojugal are tightly fused hiding the actual sutures. Since there is no chance to access the visceral side of the complex, it is difficult to estimate the shape of these bones. As indicated by E. Vorobyeva (Воробьева, 1977, p. 20) and observed by the author these bones fuse to a different degree in various individuals of tristichopterids and can not be therefore considered to be a significant feature in systematics. The squamosal-


Fig. 3. Eusthenopteron kurshi sp. nov. Structure of the head: A, specimen LDM G 291/23 in lateral view; B, reconstruction after the same specimen. Scale bar: 1 cm . Interrupted lines indicate sutures of uncertain pattern.
preopercular-quadratojugal complex is badly distorted and cracked in the type specimen. Therefore, no pit lines can be distinguished. Some pore openings on the surface of the postorbital and jugal mark the position of infraorbital canal passing through these bones.

There are several fairly thin rectangular platelets preserved within the orbital opening. These elements of the sclerotic ring once partly covered the edges of the eye-ball.

Lower jaw. The proximal and distal ends of the lower jaw of E. kurshi bend upwards (Fig. 4). Lateral surface of the jaw reveals only the suture line between dentary and the infradentaries at its hind end, the other sutures are not visible. The type specimen shows some pore openings descending from the preoperculo-mandibular canal on the ventral margin of what could be identified therefore as angular and supraangular bones. The canal is well preserved in the specimen LDM G 291/61; it opens dorsally at the very end of the jaw just behind the articular area. There is another small opening, presumably for a blood vessel, between the articular and supraangular bones. None of the lower jaws of $E$. kurshi show large unornamented medioventral flanks neither on splenial nor the supraangular, observed on the
specimens of E. obruchevi (Воробьева, 1977; Table XI, Figs. 4, 5). Just behind the adductor fossa on the articular surface two distinct depressions can be recognised, which suggests that the posteroventral corner of the quadrate must have been to some degree divided into two bumps.

The mesial wall of the lower jaw is formed by the prearticular, the surface of which is finely serrated. Between the prearticular and the dentary there are three coronoids holding a larger fang and on their lateral edge a row of small teeth, all of which are of the same size. This differs from the condition observed on the lower jaws in E. saevesoederberghi where at least one of the lateral teeth on the posterior coronoid tends to be remarkably larger than the others (Jarvik, 1937; Fig. 9).

The anterior coronoid does not reach the anterior end of the prearticular. As a result the Meckelian bone is visible on the bottom of precoronoidal fossa. The Meckelian bone fuses to the dentary forming the front end of the jaw. Dorsolaterally to the symphysial surface where the two rami of the lower jaw meet there is a small convex area where the parasymphysial dental plate is attached. As far as the preservation of the bone in specimen LDM G 291/13 allows judging


Fig. 4. Eusthenopteron kurshi sp. nov. Reconstruction of the lower jaw in mesial view. Scale bar: 1 cm . Interrupted lines indicate sutures of uncertain pattern.


Fig. 5. Eusthenopteron kurshi sp. nov. Cleithrum (LDM G 291/62): $\mathbf{A}$, in lateral view; $\mathbf{B}$, mesial view showing the scapulocoracoideum. Scale bar: 1 cm .
the shape of the plate, it is a small and elongated bone with a narrow lateral corner. It holds a number of small diffusely spread teeth which are all of the same size.

Operculo-gular series of E. kurshi are only preserved in full in the type specimen (Fig. 3). The gular is a slender triangularly shaped bone as in other early tristichopterids. Laterally it is overlapped by a row of submandibulars of which only the posterior is partly preserved revealing the overlap area on the submandibulo-branchiostegal plate.

The gill cover is formed of the upper element (opercular) and the lower (subopercular). It is peculiar feature in E. kurshi that the opercular is twice as high as the subopercular. It is just slightly higher than the latter in T. alatus (Traquair, 1875; Fig. 6). Both bones are of equal height in E. foordi.

Anteriorly the opercular bones are overlapped by bones of the cheek plate whereas dorsally overlapped by the postspiracular, a bone unique for tristichopterids. The postspiracular is attached to the tabular and lateral extrascapular.

Postcranial skeleton and the scale cover. Of the bones of the shoulder girdle the cleithrum is well preserved both in the holotype and as a detached bone (LDM G 291/62) (Fig. 5). Its dorsal lamina displays rather reticular ornamentation on the bone surface while the medioventral extension is covered in fine rounded tubercles apart from the area overlapped by the clavicle. The latter is unfortunately badly damaged and therefore poorly known.

Dorsally the cleithrum is attached to the cranial roof through the anocleithrum and the supracleithrum. The specimen LDM G 291/62 shows the structure of the inner skeleton as well. The scapulocoracoid by its shape and structure is typical to that for tristichopterids. In general, it is attached to the cleithrum at three separate points. The caudally facing rough surface held the proximal end of the humerus. Above and beneath the glenoid process lie supraglenoidal and supracoracoidal openings.

The axial skeleton is almost entirely hidden behind the scale cover. Just behind the head there are a few ventral arches identical to those described in other tristichopterids (Andrews and Westoll, 1970a; 1970b).

## DISCUSSION

In terms of body proportions there are only a few related species represented by more or less complete skeletons to allow any comparisons. Also, it is uncertain how comparable are individuals of the same size/age group but representing different species. Nevertheless, some observations can be made. The comparison of body proportions showed in Table 1 is based on the measurements made on the type specimen of E. kurshi and the body measurement data of E. foordi published by H.-P. Schultze (Schultze, 1984). Selected for comparison were only those individuals of
E. foordi whose total length corresponds to that of LDM G $291 / 23$. The results show that in $E$. kurshi the first and the second dorsal fins and the pelvic fins are positioned more caudally than they are in E. foordi, the difference being $36.5,18.2$ and $25.9 \%$. The limited number of complete skeletons does not allow estimating the intraspecific variability nor are the differences sufficiently supported statistically in terms of significance.

Yet another approach has been testing the ratios of structures in the skull. There has been a debate for decades on distinction between Eusthenopteron and an earlier tristichopterid genus Tristichopterus known from the type species $T$. alatus also represented by some complete skeletons. Initially it was suggested (Jarvik, 1937) that the parietal/ postparietal length ratio along with the proportions of the caudal fin (discussed below) should be used as the generic characters. In T. alatus the parietal shield is 1.4 times longer than the postparietal, in contrast to 1.7-1.85 in Eusthenopteron taking $E$. foordi as a good example known from many complete skeletons already by that time. Later, data on other species were added: E. traquairi ~ 1.85, E. saeve-soederberghi ~ 1.95, E.? dalgleisiensis at least 2.00 (Jarvik, 1950). During the following years J. Long has studied the parietal/postparietal length ratio changes in different genera of osteolepiforms over the Devonian (Long, 1985). He pointed to the trend forwards increasing relative length of the parietal in later forms of tristichopterids in comparison to the earlier representatives of the family. According to this observation E. kurshi by its parietal/ postparietal ratio at 1.57 fits well as an interme diate between T. alatus and Eusthenopteron species.

Discussing the proportions of the cranial roof and its applicability in systematics it is important to mention some studies on examining the growth pattern in sarcopterygian fishes: how does the ratio change over the growth of individuals, again using E. foordi as an example (Thomson and Hahn, 1968; Schultze, 1984). Thomson and Hahn state that the growth of the parietal and postparietal shields runs isometrically throughout the ontogeny. This is in general supported also by H.-P. Schultze, who still points to the fact that parietal tend to grow longer more rapidly, but this appears to be difficult to prove it as the standard deviation within each size class is too large. Schultze suggests using of another ratio instead of the one chosen by E. Jarvik-to compare the length of the parietal relatively to the total length of the cranial roof including extrascapular bones as well, which he claims to be a more reliable ratio persistent throughout various size/age groups. In $E$. kurshi this ratio is 0.34. Full applicability of parietal/postparietal ratio was later doubted by E. Jarvik himself (Jarvik, 1985). Thus, the only reliable character left to distinguish Tristichopterus and Eusthenopteron is the ratio of caudal fin lobes, also supported by some recent studies (Ahlberg and Johanson, 1997). The pattern of caudal fin proportions seen in E. kurshi is fairly similar to that of Tristichopterus alatus. However, the character is sometimes difficult to estimate adequately due to distortion of the structures during the
burial of remains-the dorsal and ventral lobe lepidotrichia can be spread to a different degree, thus influencing the measurements. Thus, the division of Tristichopterus and Eusthenopteron is rather uncertain especially when dealing with disarticulated remains of tristichopterids. Additional material and wider examination of the group is badly needed to look for quantitative rather than qualitative characters. It cannot be excluded that the tristichopterid species discussed above belong to the same genus, Tristichopterus, which has priority.

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## JAUNA DEVONA TRISTIHOPTERĪDU (PISCES, SARCOPTERYGII) SUGA NO LATVIJAS

Aprakstīta jauna tristihopterīdu suga Eusthenopteron kurshi sp. nov., kas ir senākais līdz šim konstatētais dzimtas pārstāvis Galvenā devona lauka teritorijā. Fosilijas atrastas Latvijā, Lodes mālu karjerā, vēlā Živetas/agrā Franas laikmeta nogulumos. Iegūts viens vesels skelets un vairāki atsevišķi galvas un plecu joslas skeleta kauli. Salīdzinoši nelielais parietālā vairoga garums smadzeņu kapsulas pārsegā un visai asimetriskā astes spura ir pazīmes, kuras tiek uzskatītas par tristihopterīdu primitīvāko pārstāvju raksturīgākajām iezīmēm. Zvīņas kaula (squamosum) visai tālu uz priekšu izvirzītais priekšējais stūris un vāka kauls (operculum), kas ir divreiz augstāks par zemvāka kaulu (suboperculum), ir dažas no aprakstītajai sugai tipiskajām pazīmēm.

