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THE ENDOSKELETON OF SHOULDER GIRDLE IN PTYCTODONTS (PLACODERMI)

Two Late Devonian ptyctodonts *Chelyophorus* and *Ctenurella* from the central and northwestern regions of the East European Platform have revealed an endoskeletal shoulder girdle, consisting of two ossifications. This phenomenon is so far unique in the representatives of the class Placodermi. The structure of the girdle and the probable way of the attachment of the pectoral fin in these ptyctodonts are considered in the present paper.

In placoderms, including ptyctodonts, the endoskeleton of the pectoral girdle, the scapulocoracoid, was known to consist of one ossification only. This ossification was specially studied by E. Stensiö (1959, 1969) in a great number of placoderms. In ptyctodonts the scapulocoracoid has become better known thanks to the papers by T. Ørvig (1960) and R. S. Miles and G. C. Young (1977). Three basal plates were shown to support the pectoral fin in *Ctenurella gladbachensis* (Ørvig, 1960, Fig. 4B; 1962, Fig. 2A), whereas in *Ct. gardineri* articular areas were indicated for two basals, respectively (Miles, Young, 1977, Fig. 29). In the first case another placoderm, *Pseudopetalichthys*, was used for comparison; according to F. Broili (1933, Figs. 3, 5) it possessed three basal elements. Later W. Gross, redescribing Broili's specimen, could establish the presence of two basals only (Gross, 1962, Fig. 7).

Two of us (E. M.-K. and A. I.) discovered several specimens of the anterior lateral plates with a part of the endoskeleton attached to them when studying *Ctenurella pskovensis* (earlier *Chelyophorus pskovensis* Obr.). Numerous *Chelyophorus* specimens with perfectly preserved pectoral endoskeletons at the disposal of O. Obrucheva give evidence that in this form the endoskeleton consisted of two distinct ossifications: the upper one, scapula, and the lower one, coracoid. As the lower margin of the apparent scapula in *Ctenurella* lacks any trace of fracture, there is every reason to conclude that in this ptyctodont also both ossifications existed separately.

Chelyophorus material includes some anterior lateral plates with the scapula attached to them and other more common specimens consisting of these ossifications and a ventral exoskeletal element (with a large ascending lamina) together with coracoid. As to this element or plate, its interpretation is controversial in ptyctodonts. In some cases the plate was regarded as the anterior ventrolateral plate, having also many characters of the interolateral plate (Miles, Young, 1977, p. 183; Goujet,

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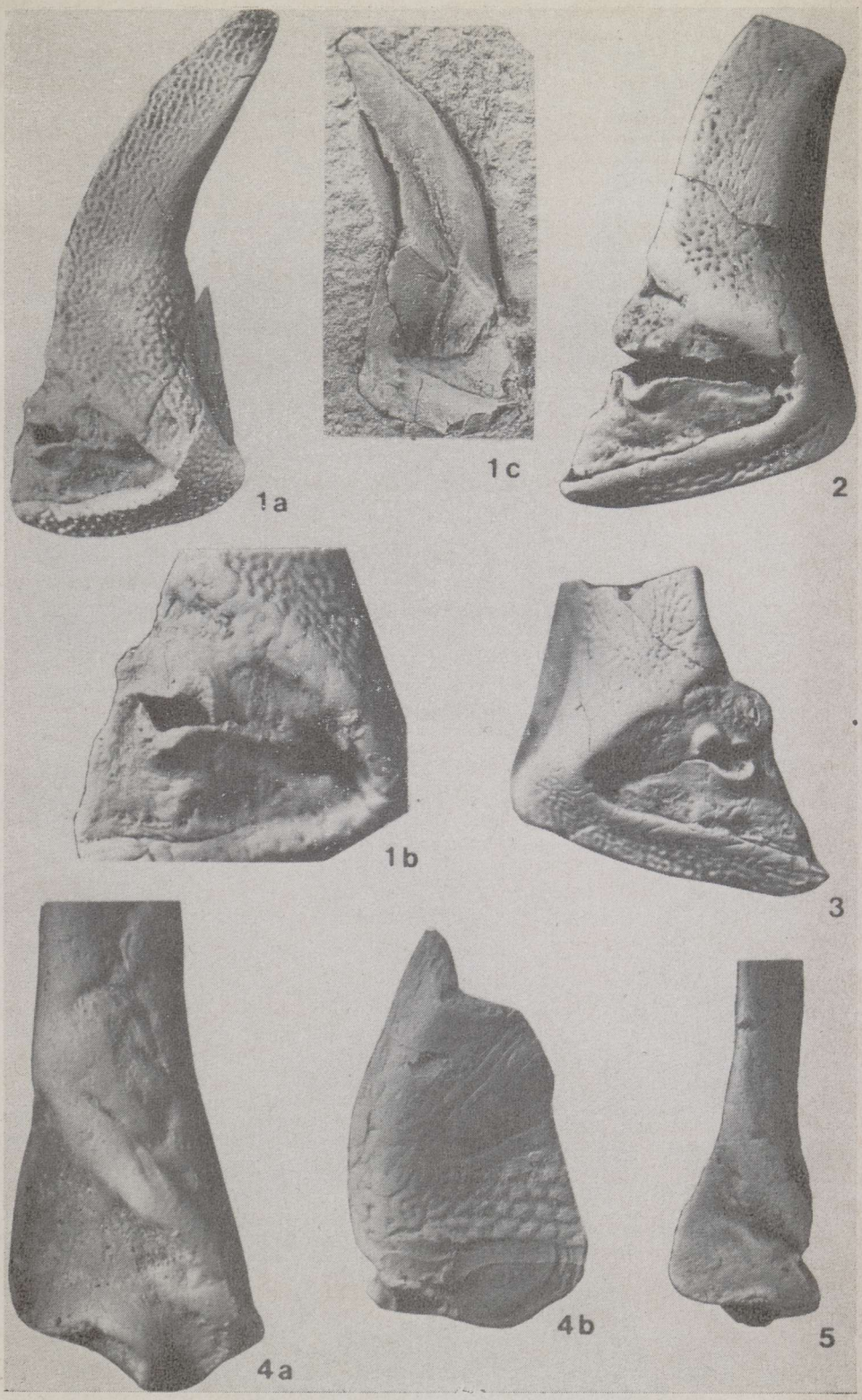
1a
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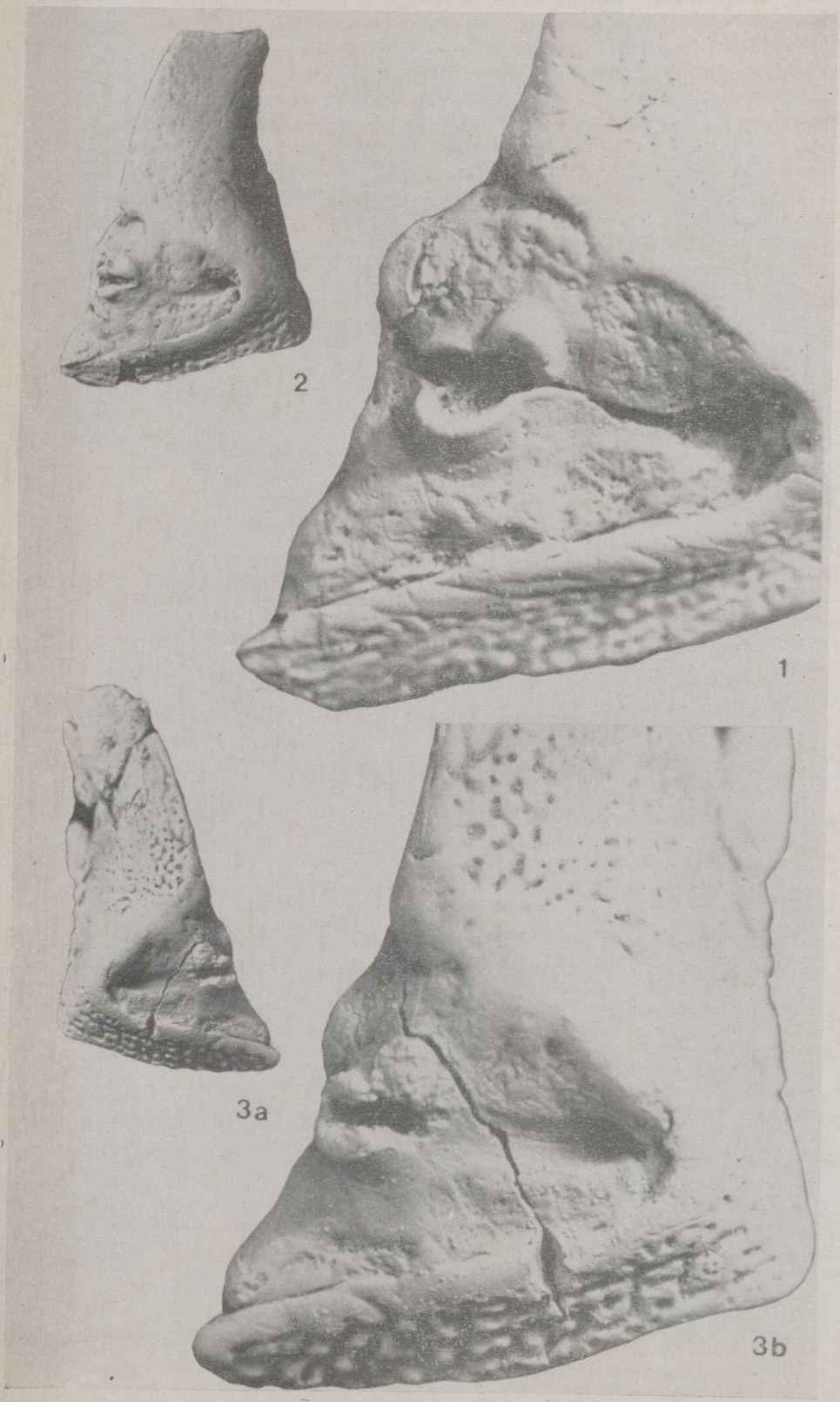
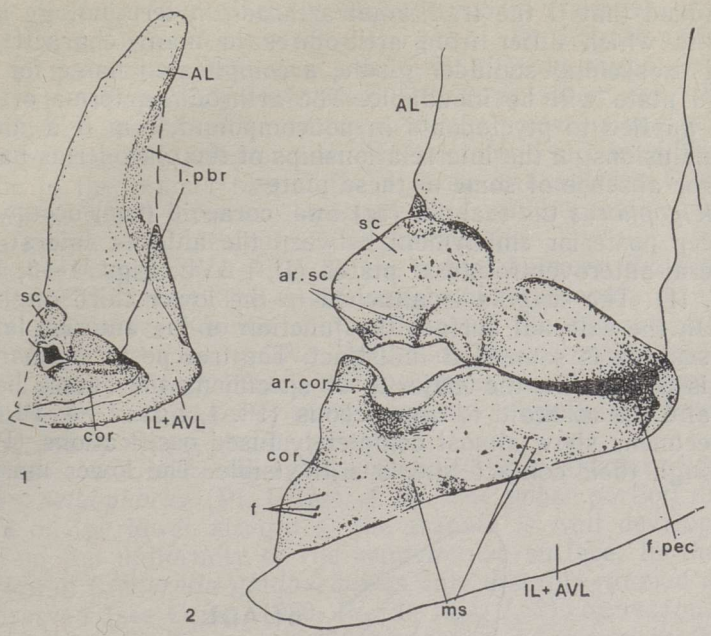
PLATE II



1984; Long, 1988). In other cases it was recognized, partly with some doubt, as the interolateral plate (Watson, 1938; Denison, 1978, 1983, 1985) or as a compound plate formed by a fusion of both plates mentioned (Stensiö, 1969; Ørvig, 1960, 1962; Марк-Курик, 1977). In this paper the latter point of view is accepted. It seems that the obviously compound plate cannot be called either interolateral or anterior ventrolateral only.



Figs. 1, 2. *Chelyophorus* sp., right lateroventral part of the shoulder girdle in external view. 1 — ×3, 2 — ×10. AL — anterior lateral plate, IL+AVL — interolateral-anteroventrolateral plate; arc. cor, ar. sc — articular surfaces on the coracoid and scapula; cor — coracoid, f — opening for nerves and vessels, f. pec — pectoral foramen, l. pbr — postbranchial lamina, ms — muscle scar, sc — scapula.

PLATE I

Figs. *1—3. Chelyophorus* sp., lateroventral part of the shoulder girdle, consisting of anterior lateral and interolateral-anteroventrolateral plates, a scapula and a coracoid. Orel Region, Central Russia, Famennian, Upper Devonian.

1a, b — right half in lateral view, *a* — ×3, *b* — ×6; LGI 4/301, coll. C. H. Pander, Orel area, *1c* — the same specimen before it was freed from rock, visceral view, ×2. *2* — right half in lateral view, ×3; PIN 3725/2, Rybnica quarry. *3* — fragmental left half in lateral view, ×4; PIN 3725/1, Rybnica quarry.

Figs. *4, 5. Ctenurella pskovensis* (Obr.), right anterior lateral plate and scapula. Frasnian, Upper Devonian.

4 — ETA GI Pi 1416; *a* — lateral view, ×6; *b* — anterior view, ×2; Meeksi Brook, SE Estonia. *5* — ETA GI Pi 1434, lateral view, ×6. Snetnaya Gora, Pskov Region, W Russia.

PLATE II

Figs. *1—3. Chelyophorus* sp., lateroventral part of the shoulder girdle. Orel Region, Central Russia, Famennian, Upper Devonian.

1 — left half, the same specimen as in Pl. I, fig. *3*, ×10 (reverse view). *2* — right half in lateral view, ×4; PIN 2657/74. *3* — left half in lateral view; *a* — ×4, *b* — ×10 (reverse view); PIN 2657/73.

It possesses a ventral wall too long for an interolateral plate of arthrodires, and a high ascending (postbranchial) lamina with a specific ornamentation completely unknown in an arthrodiran anterior ventrolateral plate. In *Ctenurella* the ornamentation, consisting of large simple tubercles is well developed, in *Chelyophorus* it is almost lacking. The length of the ventral lamina of the compound plate somewhat exceeds that of the postbranchial one in *Ctenurella* and more notably in *Chelyophorus*. It can be added that if the traditional arthrodiran terminology is used for ptyctodonts which differ from arthrodires in many characters, e. g. in the short exoskeletal shoulder girdle, a complicated name for the above compound plate will be inevitable. The arthrodiran terms of the plates could be applied to ptyctodonts in noncompound form if it did not lead to the conclusions on the interrelationships of the placoderms based on the presence or absence of some of these plates.

In *Chelyophorus* the scapula (sc) and coracoid (cor) occupy the space in the deep posterior embayment between the anterior lateral (AL) and interolateral-anteroventrolateral plates (IL+AVL, Figs. 1—3; Pl. I, figs. *1—3*; Pl. II). The scapula is attached to the lower third of the anterior lateral. On the external surface the junction of the anterior lateral plate and the scapula is somewhat indistinct. The free posterior margin of the scapula is convex. In the majority of specimens the suture between the scapula and the coracoid is conspicuous (Pl. I, figs. *1—3*; Pl II, fig. *1*). Some specimens show almost completely fused ossifications (Pl. II, figs. *2, 3*) though their contact line is still visible. The lower margin of the

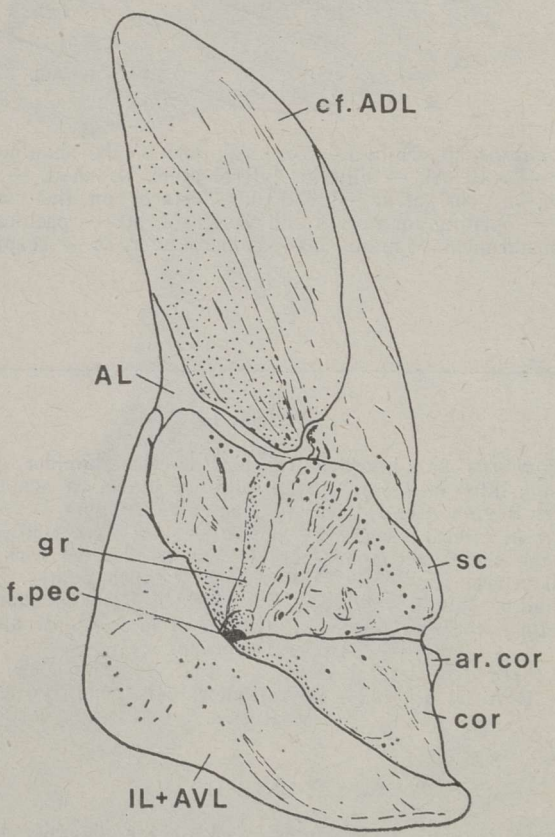


Fig. 3. *Chelyophorus* sp., right lateroventral part of the shoulder girdle in visceral view, based on PIN 2657/229 and 2657/72 (upper portion), ×5. cf. ADL — contact face for anterior dorsolateral plate, gr — groove. For the remaining abbreviations see Fig. 1.

coracoid and the lateral edge of the ventral wall of the interolateral-antero-ventrolateral plate exhibit a distinct suture. The external surface of the scapula and the coracoid are pierced by numerous minute openings for nerves and vessels (Fig. 2, f). Short grooves can be considered as the muscle scars (Fig. 2, ms). They resemble much the scars on the external face of the scapulocoracoid in the acanthothoracid *Weejasperaspis gavini* (White, 1978). At the anterior end of the suture of the scapula and the coracoid a small pectoral foramen, about 1 mm in diameter, occurs (Fig. 2, f. pec). Not far from the posterior margin of the scapula and the coracoid and at their connection two semilunar slightly rough surfaces are positioned, almost opposing each other (Fig. 2, ar. sc, ar. cor). The upper, scapular surface consists of two lobes, with the posterior one being somewhat smaller than the anterior one. A thickening runs from the anterior larger lobe to the contact line of the scapula and anterior lateral plate. These surfaces which form one structure evidently served as an articular area for a single basal element of the pectoral fin.

On the visceral surface (Fig. 3) the suture between the scapula and the coracoid is indistinct. The upper margin of the scapula in its anterior two thirds almost reaches the contact face for the anterior dorsolateral plate (cf. ADL). A wide groove (gr) runs downwards, ending at the pectoral foramen (f. pec). There are numerous small openings, particularly at the upper and posterior margins of the scapula, and several short grooves caused by nerves and/or vessels.

The scapula of *Ctenurella pskovensis* exhibits a structure very similar to that in *Chelyophorus* (Pl. I, figs. *4*, *5*). The upper portion of the articular area on the lower margin of the scapula is well developed. Difference lies in the uniformity of the semicircular surface. In the pectoral endoskeleton of *Ctenurella gladbachensis* only a single rimmed depression can be observed (see Ørvig, 1960, Pl. 26, figs. *1*, *3*), corresponding most probably to the articular area in *Chelyophorus*. According to R. S. Miles and G. C. Young (1977) two specimens of *Ctenurella gardineri* show a single perichondrally-ossified tube-like element lying adjacent to the scapulocoracoid that is thought to be a basal. It is worth noting that an articular area for an evidently single basal element of the pectoral fin is known also in the acanthothoracids *Weejasperaspis* (White, 1978, Figs. 4, 18; Pl. II d), *Radotina* (Gross, 1959, Fig. 4; Pl. 5, figs. *3*, *4*), and *Romundina* (Ørvig, 1975, Pl. 5, figs. *8*, *9*). In the latter form the fossa for the attachment of the ventral musculature of that fin (f. mv) was well developed.

It can be concluded that in ptyctodonts *Chelyophorus* and *Ctenurella* the endoskeleton of the pectoral girdle consisted of two separate ossifications, the scapula and the coracoid, thus revealing a unique feature in placoderms. The pectoral fins supported by a single basal element had a narrow base. As their scapula and coracoid with the articular area were faced laterally and there were no spinal plates to restrict the anterior movement, the pectoral fins could rotate freely in a wide extent. This, undoubtedly, made the fishes largely manoeuvrable.

Material. Specimens from the collections of St. Petersburg Mining Institute (LGI), Paleontological Institute of the Academy of Sciences of the USSR (PIN), Moscow, and Institute of Geology of the Estonian Academy of Sciences (ETA GI), Tallinn, have been used in the present research.

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PTÜKTODONTIDE (PLACODERMI) ÕLAVÖÖTME SISETOES

Hilisdevoni ptüktodontide *Chelyophorus* ja *Ctenurella* (klass Placodermi e. rüükalad) materjali põhjal, mis pärineb Ida-Euroopa platvormi leiukohtadest (Orjoli ja Pihkva oblastist ning Eestist), oli võimalik kindlaks teha mitmeid iseärasusi nende kalade õlavöötme ehituses. Erinevalt kõikidest teistest plakodermidest, kelle õlavöötme sisetoeseks oli kompaktne luumoodustis (skapulokorakoid), koosnes nimetatud ptüktodontide sisetoes kahest iseseisvast osast — skapulast ja korakoidist, mille vaheline õmblus on hästi jälgitav. Õlavöötme tagumisele osale kinnitus üksainus basaal. Et skapula ja korakoidi välimine pind oli paralleelne kala küljega ning eespool puudus uime liikumist piirav spinaalplaat, siis võis rinnauim vabalt liikuda igas suunas. Sellise õlavöötme ja rinnauime ehituse tõttu olid kirjeldatud ptüktodondid väga manööverdamisvõimelised.

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ЭНДОСКЕЛЕТ ПЛЕЧЕВОГО ПОЯСА ПТИКТОДОНТОВ (PLACODERMI)

На основании птиктодонтов *Chelyophorus* и *Ctenurella* (класс Placodermi) из местонахождений Восточно-Европейской платформы (Орловская и Псковская области РСФСР, Эстония) удалось выяснить ряд особенностей в строении плечевого пояса этих рыб. В отличие от плакодерм, эндоскелет плечевого пояса которых представлен, как правило, одним окостенением, у описываемых птиктодонтов он состоял из двух самостоятельных частей — скапулы и коракоида, разделенных хорошо просматриваемым швом. К задней части этих окостенений прикреплялся один базальный элемент. Поскольку внешняя поверхность скапулы и коракоида была направлена вбок, а спинальная пластинка, ограничивающая движение грудного плавника, перед этими окостенениями отсутствовала, то плавник имел широкий диапазон вращения. По этой причине рыбы этого типа обладали хорошими маневренными способностями.