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Palatoquadrate in a Devonian fish Eusthenopteron

Evidence of its dual origin

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Abstract

The palatoquadrate in *Eusthenopteron* displays certain variation concerning the extent of its com-
missural lamina, and the presence of imprints of vessels and nerves on the outer surface of this
middle part of the element. Comparison with some contemporary fishes revealed that branches
of the arteria ophthalmica magna or of the ramus palatinus posterior VII could have produced
these imprints. The grooves are connected with canals piercing the bone along its pars
pterygoquadrata. Possible explanation is that the autopalatine and pterygoquadrate portions of
the palatoquadrate were free in early developmental stages and later become interconnected by
cartilage and bone. The dual nature of the palatoquadrate is shown to occur not only in the de-
velopment of some Recent fishes, but in extinct groups (e. g., placoderms) as well.

Key words: Crossopterygii – Skull – Development

Introduction

Generally, the palatoquadrate in *Eusthenopteron* consists of anterolateral and posterodor-
sal thickened marginal parts (termed the pars autopalatina and pterygoquadrata, respec-
tively). The two parts are connected with one another by a thin commissural lamina (sensu
JARVIK) or vinculum (sensu BJERRING). WATSON (1925: 860; 1926: 248–249) believed that
the palatoquadrate in osteolepids consisted of separate ossifications (termed the supra-
pterygoids) arisen in the palatoquadrate cartilage. According to him, there were four of
them in *Eusthenopteron*, namely the autopalatinum, epipterygoid, metapterygoid, and the
quadrate. HOLMGREN and STENSIÖ (1936: 354–355) could not confirm WATSON's state-
ment. Instead, they concluded that the palatoquadrate of *Eusthenopteron* is a single os-
sified structure extending from the pars autopalatina to the pars pterygoquadrata, and
middle part of which, along its ventral margin, is much reduced. This condition corres-
ponds to that in specimen No. P 222 reconstructed by JARVIK on the basis of grinding
series 2 (JARVIK 1954, Fig. 23 B; 1981, Fig. 46 B). ARRATIA and SCHULTZE (1991) do not
believe in what they call 'fenestration' of the palatoquadrate, arguing that HOLMGREN and
STENSIÖ could have been wrong in distinguishing thin dermal bone from thin chondral
bone in serial sections. Isolated palatoquadrates of some other specimens (WATSON 1926,
Fig. 34; JARVIK 1972, Fig. 26 A; ARRATIA and SCHULTZE 1991, Fig. 3) indicate that the com-
missural lamina extended almost up to the ventral margin of the entopterygoid (JARVIK
1980, Fig. 109; ARRATIA and SCHULTZE 1991, Fig. 31 C). Besides these differences in the
extent of the commissural lamina, there is a peculiar system of grooves and canals that can
be observed on the outer surface of the palatoquadrate in some specimens (see JARVIK
1954: 27; 1972: 73, Fig. 26 A–C; ARRATIA and SCHULTZE 1991, Fig. 3). Similar grooves were
also found in some specimens of *Holoptychius* (JARVIK 1972: 73, Figs. 33 C, E). In the
account to follow, an attempt will be made to explain variation in extent of the commis-
sural lamina (in this respect, attention will be devoted especially to available information

concerning the earliest developmental stages that might reflect evolutionary primitive condition), as well as the grooves on and canals piercing the palatoquadrate (for this sake, some contemporary forms will be taken for comparison).

Results

The specimens hitherto found to show traces of nervous or vascular system on the surface of the palatoquadrate in *Eusthenopteron* is MHNM 6-496 from the museum in Miguasha, Quebec, Canada, and an imprint of the left palatoquadrate and slightly disarticulated maxillary from Sedgwick Geological Museum, Cambridge, England. The photograph of the former was published by ARRATIA and SCHULTZE (1991, Fig. 3), and photograph of the latex cast of the latter was published by JARVIK (1972, Fig. 26 A). A detailed examination of the specimen from Sedgwick Museum and casts of both specimens resulted in following description.

Both palatoquadrates belong to large specimens. The length of the Sedgwick specimen, from the proc. apicalis to the most posterior exposed part of the commissural lamina (the head of the quadratum is not preserved), is about 100 mm. The length of the palatoquadrate in the Miguasha specimen, though only visible parts were measured, is about 140 mm. On the other hand, the palatoquadrate of the specimen that JARVIK used for the preparation of a wax model (P 222) is smaller. This can be judged from the distance between the anterior marginal crack (slightly behind the anterior margin of the posterior tectal) and
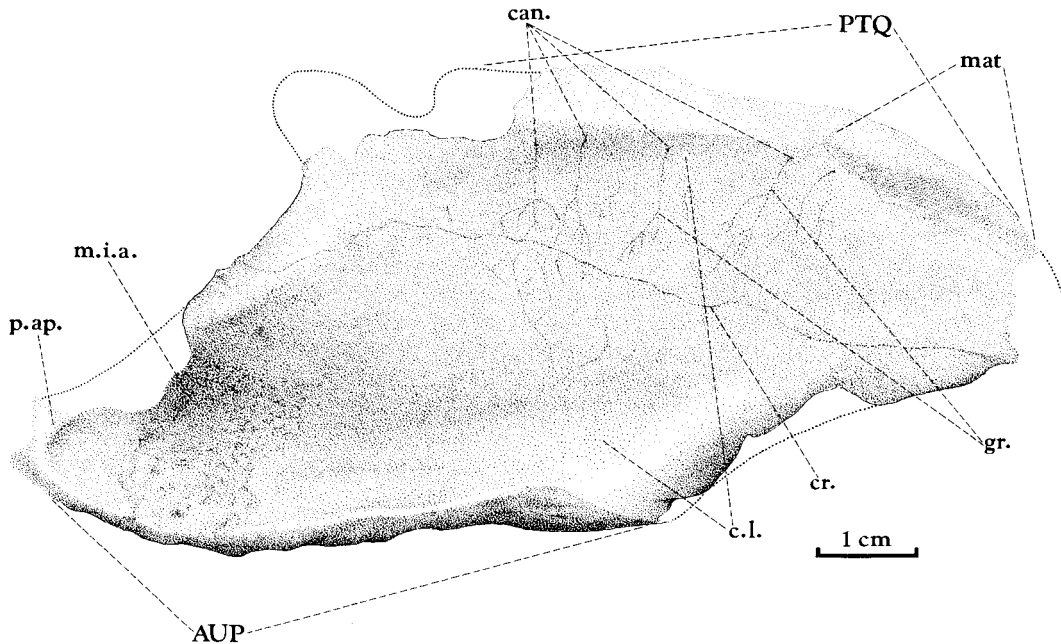

Fig 1. Left palatoquadrate of *Eusthenopteron* in lateral view. Lowermost Upper Devonian, Escuminac Formation of Miguasha, Canada. Coll. Sedgwick Geological Museum, Cambridge. AUP = pars autopalatina; PTQ = pars pterygoquadrata; can = orifices of canals arranged in a row along the pars pterygoquadrata; c. l. = extent of the commissural lamina; c. r. = crack; gr. = network of branching grooves; mat = part of pars pterygoquadrata covered by matrix; m. i. a. = area for muscle insertion; p. ap. = processus apicalis. Estimated original shape is drawn by dotted line
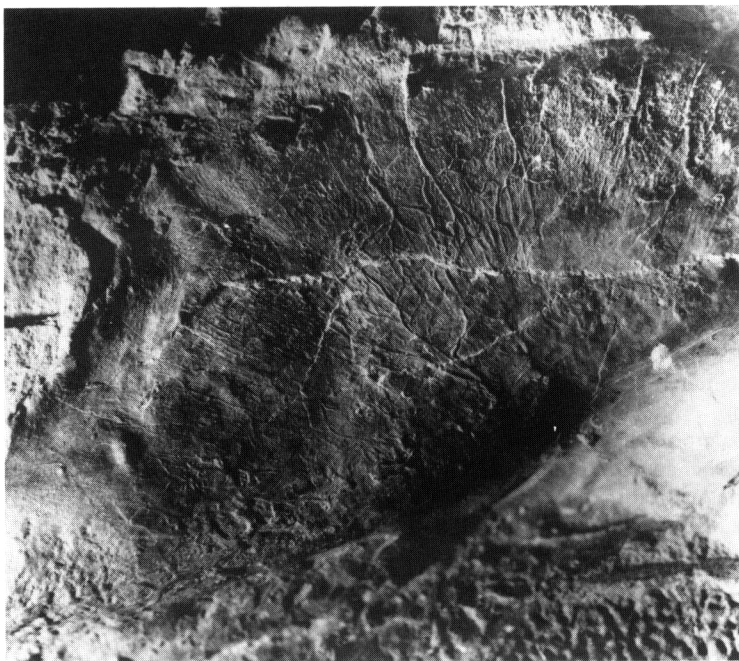
Fig. 2. Middle part of palatoquadrate of *Eusthenopteron*, showing the pattern of grooves on the surface of the commissural lamina. Same specimen as in Fig. 1

the posterior margin of the preopercular which is 82 mm (measured on the cast of the head). This distance roughly corresponds to the anterior-posterior length of the palato-quadrate. Hence, sectioned Stockholm P 222 specimen is obviously the youngest of all three.

In the Sedgwick specimen, almost entire pars autopalatina is preserved, incl. its proc. apicalis (Fig. 1). The pars pterygoquadrata is intact in its medial part. The posteroventral part of the latter is covered by matrix, and its anterior part is lacking; however, imprint in the matrix makes it possible to reconstruct its shape with sufficient accuracy. Obviously, the whole palatoquadrate, incl. its commissural lamina, was ossified. A conspicuous feature is that parallel to the middle section of the pars pterygoquadrata is a row of tiny pores from which branching grooves continue onto the surface of the commissural lamina (Fig. 2).

In the Miguasha specimen (ARRATIA and SCHULTZE 1991, Fig. 3) the anterior and post-erior ends of the palatoquadrate cannot be observed but the commissural lamina is well exposed. The ventral part of the commissural lamina is intact and obviously completely ossified. There is a net of grooves oriented towards the dorsal margin of the element, though grooves are less pronounced if compared with the Sedgwick specimen, and pores are lacking.

Similar grooves as in both specimens of *Eusthenopteron* mentioned above were found also in some specimens of *Holoptychius* (JARVIK 1972, Fig. 33 C, E). To answer the question what caused these canals and grooves I decided to dissect a specimen of *Amia calva*, and to review pertinent data from literature.

The dissected specimen of *Amia* was of 52 cm rostrocaudal length, and the dissection involved the left part of the head, to enable comparison with the investigated palatoquad-rate of *Eusthenopteron*. The palatoquadrate of *Amia* (Fig. 3) consists of three ossifications
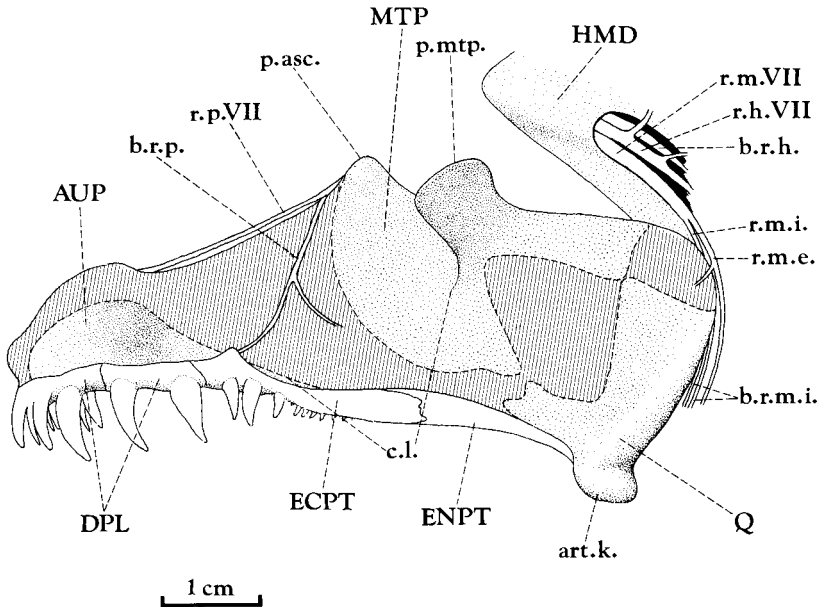
Fig. 3. Left palatoquadrate in *Amia* (NM Prague coll. No. P6V–5980). AUP = pars autopalatina; ECPT = ectopterygoid; ENPT = entopterygoid; Q = quadrate; HMD = hyomandibula; art. k. = articular knob of quadrate; b. r. h. = branch of ramus hyoideus; b. r. m. i. = branch of ramus mandibularis internus; b. r. p. = branch of ramus palatinus posterior VII; c. l. = extent of commissural lamina; p. asc. = processus ascendens; p. mtp. = processus metapterygoideus; r. h. VII = ramus hyoideus VII; r. m. VII = ramus mandibularis VII; r. m. e. = ramus mandibularis externus; r. m. i. = ramus mandibularis internus; r. p. VII = ramus palatinus posterior

– the autopalatinum, metapterygoid, and quadratum, The autopalatinum is widely separated from the metapterygoid by a thin but extensive cartilage. This cartilage continues posteriorly and separates the metapterygoid and quadratum. However, though the two latter ossifications are clearly separated from one another, there is indication that the ossification process would still continue along the anterior margin of both elements. Posteriorly, they are in contact with one another but the suture is well distinguishable. The most posterior part of the palatoquadrate is also cartilaginous but has appearance of an oncoming ossification. This will probably result in contact or fusion of the matapterygoid and quadratum in old specimens.

Ventral to the autopalatine there are two dermopalatines and the anterior part of the ectopterygoid. The latter ossification does not extend up to the quadrate. The ventromedial surface of the palatoquadrate is adjoined by the entopterygoid. This bone, however, does not cover the most posterior part of the palatoquadrate. Irregular fields with small denticles may indicate that the entopterygoid has not yet attained its definite size. The palatoquadrate cartilage exceeds the dorsal margin of this not yet fully developed entopterygoid.

The lateral surface of the posterior part of the palatoquadrate serves for attachment of the deep layer of the adductor mandibulae muscles. The fascia of insertion for these muscles continues dorsally beyond the palatoquadrate to the lateral surface of the hyomandibula, and thus separates the adductor mandibulae from the levator arcus palatini. The anterior portion of the levator arcus palatini is inserted into the deep notch between the basalis and metapterygoideus processes, on the lateral surface of the former (see also ALLIS 1897, pl. 29, Fig. 36). The m. nasalis (= levator maxillae superior 4 of ALLIS) is attached by its tendon to the dorsal outgrowth of the ectopterygoid (this outgrowth can be seen in

Fig. 3). The m. praeorbitalis (= levator maxillae superior 3 of ALLIS) is situated between the m. nasalis and the palatoquadrate cartilage.

Among the nerves that pass close to the palatoquadrate are branches of the VII cranial nerve. The r. hyomandibularis, after having passed through the hyomandibular canal, divides into a r. mandibularis (located anteriorly) and r. hyoideus (located posteriorly). In the examined specimen there was still another branch issuing from the hyomandibular canal, probably a branch of the r. hyoideus. The r. mandibularis splits into the r. mandibularis externus and r. mandibularis internus. The former runs closely behind the posterior corner of the palatoquadrate, and gives off a large branch which passes through the adductor mandibulae muscles. The latter runs underneath the posterior part of the palatoquadrate, where it divides in the dissected specimen into two parallel branches. All the branches of the r. mandibularis continue parallel to the posterior margin of the palatoquadrate onto the inner surface of the mandible. As the r. mandibularis and its branches are sensory nerves they do not come in close contact with the palatoquadrate.

Another branch of the facialis nerve is the r. palatinus. Its posterior branch, termed the r. palatinus posterior, issues from the palatine canal between the endocranium and the parasphenoid. It can be observed after removing the mucous membrane of the mouth roof. A short distance after exiting from the palatine canal it reaches the dorsal edge of the palatoquadrate, close anterior to the proc. ascendens. It then follows this edge anteriorly, exactly as in a 22 mm larva (see JARVIK 1980, Fig. 10). In the vicinity of the proc. ascendens it gives off a branch which runs onto the dorsolateral surface of the palatoquadrate cartilage and continues anteriorly, following the dermopalatine-autopalatine suture. When crossing the commissural lamina, it gives off a branch which is directed posteriorly. These branches and their terminal divisions are embedded in the superficial fascia of the palatoquadrate, and are thus in an intimate contact with that skeletal structure. Hence, statement by ALLIS (1897: 619) that the r. palatinus posterior runs in the space between the entopterygoid and the palatoquadrate, below the autopalatinum, cannot be confirmed in the dissected specimen. Perhaps there is a certain variation in the course of this nerve.

It should also be noted that within the anterior thin and transparent marginal part of the cartilage separating the metapterygoid and quadrate ossifications, there is a branching network of whitish filaments which originate close to the basal part of the anterior margin of the proc. metapterygoideus (i. e., on the bottom of the notch between the ascendens and metapterygoid processes). This branching and partly reticulated filaments are possibly terminal branches of a nerve embedded in the cartilage.

Both the r. buccalis lateralis (a branch of VII) and r. maxillaris (2nd branch of V) run forwards below the orbit, in certain distance from the palatoquadrate (see also JARVIK 1980, Fig. 10).

In *Latimeria* (MILLOT and ANTHONY 1965: 60, Fig. 26), the r. palatinus seems not to split into a posterior and anterior branches, and it has no contact with the palatoquadrate. However, in *Polypterus* (ALLIS 1922: 280–281) a branch is given off from the base of the r. palatinus that lies in the dense connective tissue which binds the palatoquadrate to the lateral edge of the parasphenoid. Then, this branch splits into two branches both of which run ventrally between the entopterygoid and the palatoquadrate cartilage. The main stem of the r. palatinus continues within the tissue adjoining the dorsomedial edge of the palatoquadrate. Here, this nerve stem gives off a branch which runs anterolateroventrally along the internal surface of the palatoquadrate, between it and the entopterygoid and ectopterygoid. Thus, the branching pattern of the r. palatinus recalls that in the above-described specimen of *Amia*. Another peculiarity in *Polypterus* is that, in contrast to *Amia*, the r. mandibularis internus either passes through a notch or a foramen at the posterior corner of the palatoquadrate (ALLIS 1922, Fig. 47).

Although the dissection of *Amia* revealed that nerves have the most intimate contact with the palatoquadrate, the pattern of grooves on the surface of the investigated

palatoquadrate of *Eusthenopteron* suggests that blood vessels might also be considered. Returning to *Amia* (ALLIS 1900, 1908, 1912; DE BEER 1924), the pseudobranchial arterial circulation may be taken into account because the pseudobranch in an 11–12 mm larva is already well developed and later shows no signs of arterial degeneration. This organ lies near the dorsal ·edge of the palatoquadrate. Its efferent pseudobranchial artery (also termed efferent mandibular by ALLIS, anterior carotid by PARKER, and part of the afferent spiracular and carotis interna anterior by DOHRN) has relations to the palatoquadrate. This artery passes outward in the angle between the anterior edge of the hyomandibula and the posterior edge of the palatoquadrate, and then turns ventrally and runs along the lateral surface of the latter. In a slightly older larva, however, the artery runs through a narrow space between the palatoquadrate and hyomandibula, lying between the two mandibular branches of the facialis nerve. Afferent pseudobranchial arteries (according to ALLIS, there are two of them – the primary one in early developmental stages, and the secondary one that replaces the primary in the adult), have no close relation to the palatoquadrate. Embryologically, this mandibular arterial arch takes its origin from the so-called prespiracular arch which is complete in early stages (e. g., 6 mm). This arch is connected with the postspiracular one by a commissure lying ventral to the spiracular cleft. This connection atrofied in the 12 mm larva. However, a similar commissural artery is probably the arteria ophthalmica magna (also termed choroidalis by DOHRN) which arises from the efferent pseudobranchial artery and runs anteriorly to supply the choroid gland; this gland has been considered a possible remnant of a premandibular gill. ALLIS (1908: 114) quotes RAFFAELE who, in larval selachian, even found a possible homologue of the premandibular artery that is connected through the arteria ophthalmica magna with the mandibular aortic arch. In an 11 mm *Amia* (see DE BEER 1924, text-fig. 17), the a. ophthalmica magna is directed towards the middle part of the palatoquadrate, running between its autopalatine and pterygoquadrate parts. Thus, this is the only artery that in early developmental stages passes the area of the future commissural lamina.

Discussion

If it is accepted that the branching network of grooves on the examined palatoquadrate of *Eusthenopteron* might be caused either by the arteria ophthalmica magna or by terminal branches of the r. palatinus posterior VII that are given from this nerve after it left the palatine canal between the neural endocranium and the parasphenoid, it can be suggested that the canals which pearce the bone in a row along the pars pterygoquadrata are a consequence of an earlier evolutionary state when the autopalatine and pterygoquadrate parts still were isolated (at least partially). This hypothesis is supported by following observations.

In *Amia* (PEHRSON 1922; DE BEER 1937: 97–103), the palatoquadrate develops from two centers. The posterior one arises first and is attached to the tip of the trabecula by a strip of mesenchyme. Later, anteriorly within the tissue where the ethmopalatine articulation will form, another center of chondrification arises. These two cartilages are connected with one another by procartilage for some period of development. ARRATIA and SCHULTZE (1991 and pers. comm.) could not confirm this statement but the reason is that they investigated stainable, i. e., developmentally more advanced stages, not the precartilaginous ones. In the adult, both centers are ossified; the space between them, however, remains cartilaginous. Thus in *Amia*, the palatoquadrate displays a certain duality in its developmental origin; this duality could be (but not necessarily is) expressed by the autopalatine and metapterygoid-quadrate ossifications. Referring to *Nesides*, BJERRING (1977) concluded that the two ossifications are separate and distinct entities in the coelacanthiforms. Moreover, NORMAN (1926: 444) stated that the anterior part of the palatoquadrate in teleosts chondrifies independently from the posterior one. ARRATIA and SCHULTZE (1991)
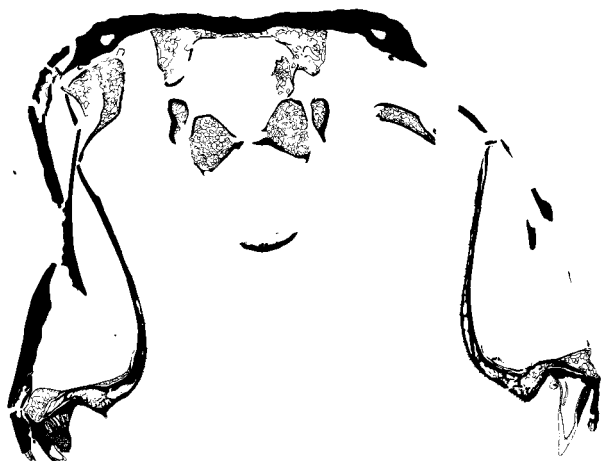
Fig. 4. Transverse section (No 227 A) through the skull of *Eustehnopteron* closely behind the orbit, to show the extent of the commissural lamina in this specimen. Lowermost Upper Devonian, Escoumenac Formation of Miguasha, Canada. Specimen No P 222, Department of Paleozoology, Swedish Museum of Natural History, Stockholm
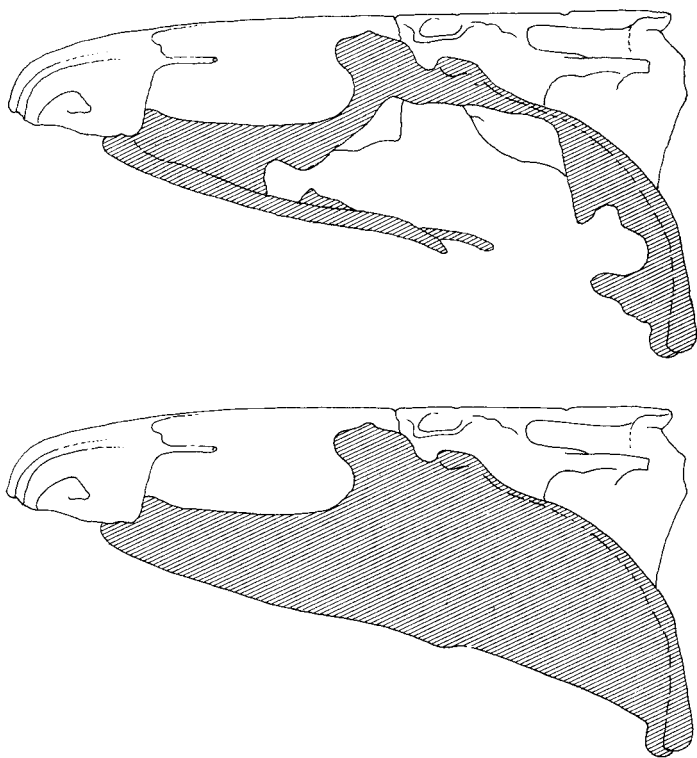

Fig. 5. Sketch to show two possible developmental stages of the palatoquadrate in *Eusthenopteron.* Younger stage with not yet fully ossified palatoquadrate (above), and older stage (below). Based on data from JARVIK (1954, 1980) and BJERRING (1977)

confirm that for siluroids. Furthermore, DENISON (1978: 5, Fig. 3 E) found that the pars autopalatina is separate from the quadrate in some placoderms. The metapterygoid-quadrate in *Amia* displays certain variation in the degree of ossification. Whereas in the dissected specimen described above, the metapterygoid and quadrate are separated by a strip of cartilage (though this cartilage displays some signs of ossification), the whole posterior part of the palatoquadrate, except for the most posterior corner, was ossified (both elements being divided only by a suture) in the specimens examined by ALLIS (1897, pl. XX, Figs. 1, 2) and JARVIK (1980, Fig. 40 A). Thus it would seem that the degree of ossification in the posterior part of the palatoquadrate of *Amia* is a developmental feature, and that the middle part remains cartilaginous regardless the age of the individual.

A similar development of the palatoquadrate is indicated also in *Eusthenopteron*, though in the adult it is fully ossified, as indicated by preserved isolated palatoquadrata. However, an investigation of the serially ground sections of specimen P 222 (Fig. 4; see also JARVIK 1954, Figs. 6 A, 12 B) revealed that there was a large vacuity with irregular margins between the pars autopalatina and pars pterygoquadrata posteriorly (Fig. 5). As may be judged from the sections this vacuity is of about the same extent on both sides of the skull. This suggests that it is natural, not an artefact or result of wrong interpretation. Most probably it was filled with thin layer of cartilage in living animal, as it is in *Amia*. One can assume that cartilage was substituted by bone in the fully grown individual. This presupposition seems to be supported by the larger size of completely ossified palatoquadrates.

All this suggests that in earlier developmental stages, when the pars autopalatina and pars pterygoquadrata were still separated by a mesenchymatic sheet and the palatal surface was not yet adjoined by the entopterygoid, either the arteria ophthalmica magna or the r. palatinus posterior VII (or its branches) passed towards the lower margin of the elongated pterygoquadrate element (which was cartilaginous and later ossified). By subsequent chondrification and ossification of the mesenchymatic commissural lamina, the branches of the artery or nerve were enclosed into delicate canals. These, however, maintained their former arrangement following the lower margin of the pars pterygoquadrata, though they could be closed in large (= old) specimens.

Conclusions

1. The row of canals piercing the palatoquadrate in the adult *Eusthenopteron*, and the branching network of grooves on the outer surface of its commissural lamina may be caused either by branches of the arteria ophthalmica magna (which might represent an anastomosis between ancient premandibular and mandibular arterial arches), or by branches of the ramus palatinus posterior VII.

2. Although the palatoquadrate in a fully grown *Eusthenopteron* is completely ossified, the space between its autopalatine and pterygoquadrate parts was filled in considerable extent by cartilage in younger individuals, as documented by Stockholm P 222 specimen. Hence, the palatoquadrate may reflect some developmental changes.

3. The palatoquadrate of many osteichthyans arises embryologically from two separate centers. This dual origin may be reflected in the adult by an anterior and a posterior ossification connected by cartilage or, in the fully ossified individuals, by traces of vessels or nerves that are enclosed in the portion of the palatoquadrate that connects its autopalatine and pterygoquadrate parts.

4. Adult representatives of some extinct groups (e. g., placoderms) also have their palatoquadrates divided into the autopalatine and pterygoquadrate parts.

5. In sum, embryological and paleontological data suggest that the palatoquadrate has a dual origin, and that morphological variation in the palatoquadrate of *Eusthenopteron* reflects this dual nature.

Acknowledgements

Zusammenfassung

Das Palatoquadratum beim devonischen Fisch Eusthenopteron. Beweise seines doppelten Ursprungs

Das Palatoquadratum bei *Eusthenopteron* variiert im Umfang der Kommissurallaminae, und in der Anwesenheit der Gefäß- und Nervenabdrücke auf der äußeren Seite des mittleren Teiles dieses Elements. Der Vergleich mit manchen rezenten Fischen deutet an, daß die Ästchen der Arteria ophtalmica magna oder des Ramus palatinus posterior VII diese Abdrücke verursachen könnte. Die Rinnen sind mit den Kanälchen, die den Knochen längs der Pars pterygoquadrata durchbohren, verbunden. Mögliche Erklärung für diese Situation ist, daß die Autopalatinum- und Pterygoquadratumteile des Palatoquadratums im früheren Stadium unabhängig und später nur mit der Knorpel und mit dem Knochen verbunden waren. Die doppelte Natur des Palatoquadratums ist nicht nur in der Ontogenie der rezenten Fische, sondern auch in einigen vollständig ausgestorbenen Gruppen (z. B. Placodermi) manifestiert.

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