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Hyobranchial Skeleton and Hypobranchial Muscles of Rhipidistians

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Abstract—The hyobranchial skeleton of the porolepiform rhipidistian *Laccognathus panderi* Gross is described. The double composition of the ceratohyal in crossopterygians is proposed. The urohyal of porolepiforms, like that of *Latimeria*, consists of cartilaginous axial and membranous peripheral portions. The differences between porolepiforms and osteolepiforms in the structure of the hyobranchial skeleton, particularly, in the shape of the urohyal are attributable to different arrangements of the hypobranchial muscles. Porolepiforms and coelacanths have retained the coracomandibularis muscle inherited from early gnathostomes, whereas the same muscle of osteolepiforms was transformed into the geniohyoideus muscle. This transformation is accounted for by functional changes in the hyobranchial apparatus.

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Key words: Hyobranchial skeleton, hypobranchial musculature, Rhipidistia.

INTRODUCTION

Among the anatomical structures considered by Jarvik (1963, 1972) as evidence for the theory of diphyletic origin of terrestrial vertebrates, a significant role is played by the hyobranchial apparatus. However, the hyoid and branchial arches are extremely infrequently preserved in fossils in the condition suitable for the morphological study; in particular, two taxa examined by Jarvik (*Eusthenopteron foordi* and *Glyptolepis groenlandica*) were supplemented by the material of the hyobranchial skeleton of new crossopterygians only in the 1990s (Lebedev, 1995; Johanson and Ahlberg, 1997). Therefore, the perfectly preserved specimens of the porolepiform rhipidistian *Laccognathus panderi*[1] found in the well-known Lode locality (Vorobyeva, 1980), which enabled the hyobranchial skeleton to be examined in detail, stimulated the study of this structure in rhipidistians. This was also promoted by a possibility to examine the holotype of the osteolepidid crossopterygian *Medoevia lata* stored in the Paleontological Institute of the Russian Academy of Sciences (PIN), which also retained a number of hyobranchial elements.

In this paper, based on the comparison with various extant taxa, the major structural differences between porolepiforms and osteolepiforms in the hyobranchial skeleton are considered to be connected with different positions of the hypobranchial musculature. A functional interpretation of morphological changes in these structures, which occurred at the initial stage of the evolution of Osteolepiformes, is proposed.

MATERIAL

The specimens of *Laccognathus panderi* examined in the present study come from a quarry of the drainpipe factory Lode of the Liepa clay deposits (Latvia, 90 km northeast of Riga, vicinity of Cesys). They were collected by workers of PIN headed by E.I. Vorobyeva in the 1970s. The locality is confined to clays of the upper strata of the Gauja Horizon assigned to the Lode Formation (Kurshs and Lyarskaya, 1973; Forey et al., 2000). The Gauja Horizon is traditionally assigned to the bottom of the Frasnian Stage (Lyarskaya, 1981); however, it was recently proposed that it could have belonged to the Givetian (Forey et al., 2000). The hyobranchial skeleton of *Laccognathus panderi* was studied using mostly the following specimens (all stored in PIN): PIN, no. 3547/7 (almost complete skeleton of the head and anterior part of the trunk); no. 3547/12 (ventral region of the hyobranchial skeleton with clavicles, open from the dorsal side); no. 3547/8 (considerably distorted skull displaying the hyobranchial skeleton from the ventral side); no. 3547/26 (ventral region of the hyobranchial skeleton with clavicles, open from the ventral side); no. 3547/24 (almost complete cranial skeleton of a small fish); and no. 3547/22 (isolated ceratohyale). For the data on the holotype of *Medoevia lata*, see Lebedev (1995).

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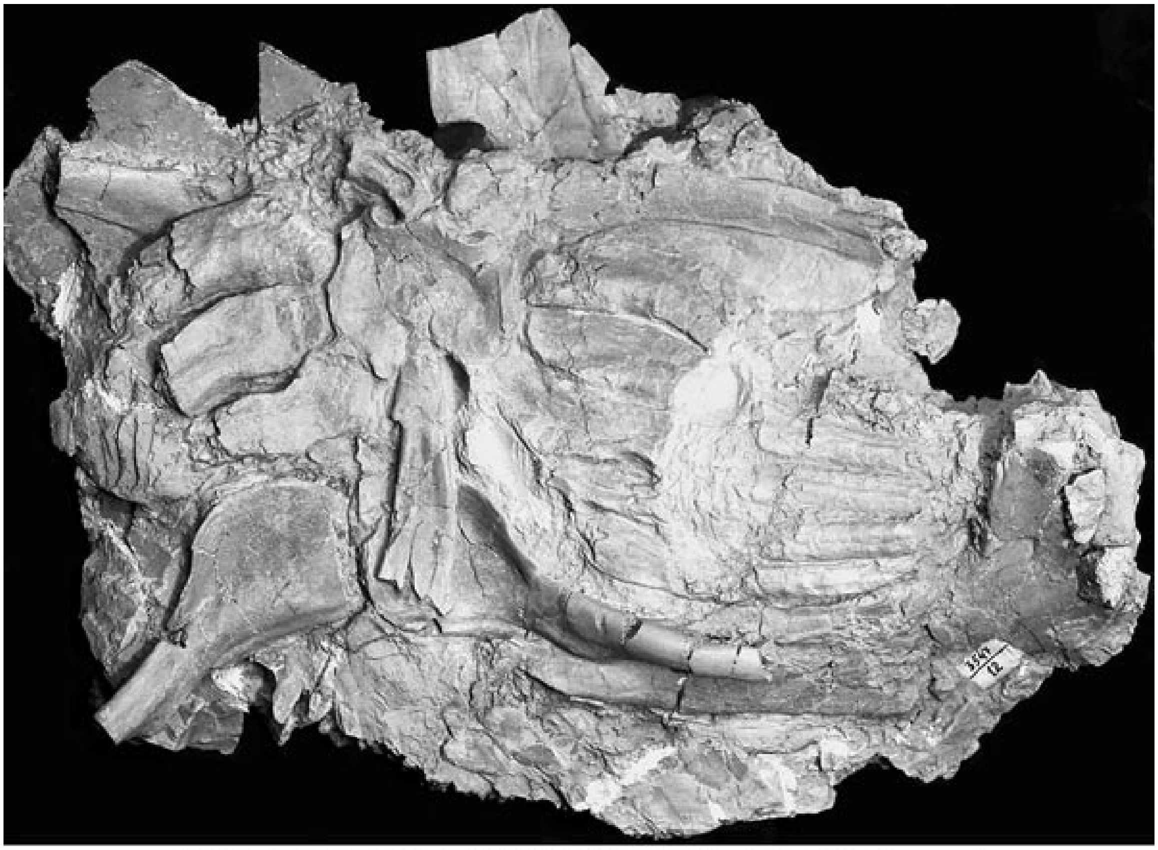
[1] At present, *Laccognathus* from Lode is established by Vorobyeva (2006) as a distinct species.

Plate 9



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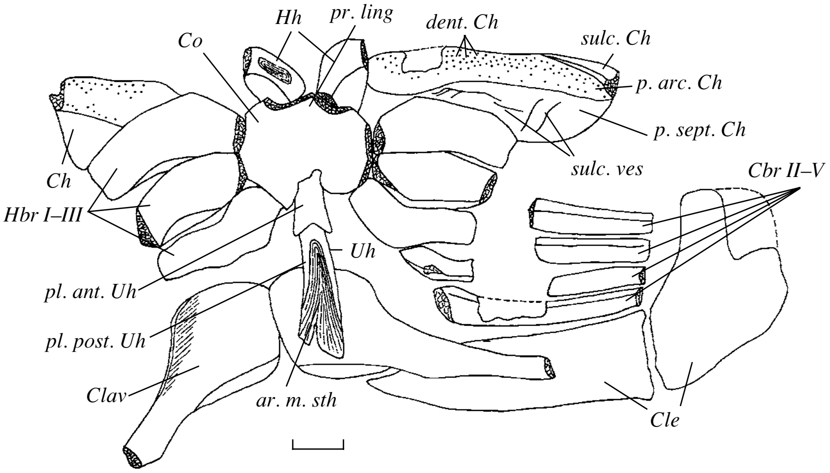


Fig. 1. *Laccognathus panderi* Gross, specimen PIN, no. 3547/12, ventral region of the hyobranchial skeleton, dorsal view. Designations: (*Cbr*) ceratobranchiale, (*Ch*) ceratohyale, (*Clav*) clavicle, (*Cle*) cleithrum, (*Co*) copula, (*Hbr*) hypobranchiale, (*Hh*) hypohyale, (*Uh*) urohyale, (*ar. m. sth*) attachment area for the sternohyoideus muscle, (*dent. Ch*) denticle on the internal surface of the ceratohyal, (*p. arc. Ch*) arched region of the ceratohyal, (*p. sept. Ch*) "septal" region of the ceratohyal, (*pl. ant. Uh*) anterior region of the dorsal plate of the urohyal, (*pl. post. Uh*) posterior region of the dorsal plate of the urohyal, (*pr. ling*) lingual process, (*sulc. Ch*) groove in the anterior margin of the ceratohyal, and (*sulc. ves*) imprints of blood vessels (?). Scale bar, 2 cm.

MORPHOLOGICAL DESCRIPTION OF THE HYOBRANCHIAL SKELETON

Laccognathus panderi Gross, 1941

Plate 9, figs. 1 and 2; Plate 10, figs. 1 and 2

The basihyale and basibranchialia form an integrated bone named below the copula. The copula (Figs. 1–3, *Co*) is rounded multangular in outline, with the medial length approximately equal to the greatest width, which is at the boundary between the articular facets for hypobranchialia of the first and second branchial arches. The posterior region of the copula narrows and is somewhat elongated in the area of articulation with branchial arch III. In the middle of the anterior margin, the copula forms a small pointed projection corresponding to the processus lingualis of *Glyptolepis* (Jarvik, 1963), which is distinct on both the dorsal (Fig. 1, *pr. ling.*) and ventral (Figs. 2, 3, *pr. ling.*) sides. On both sides of the projection, there are notches, which contained the distal ends of the hypohyalia. The articular facets for the hypohyalia (Figs. 2, 3, *ar. art. Hh*), which lack periosteum, face anteroventrally; their posteroventral margins come onto the lower surface of the anterior region of the copula, where they meet special ventral projections (Figs. 2, 3, *pr. art. Hh*). The lateral sides of the copula have attachment areas for hypobranchials I–III, which closely adjoin each other, while the articular notches of the hypohyals are separated from the articular facets of hypobranchials I by a relatively large space. The articular facets for hypobranchialia are shallow, ventrolaterally oriented fossae (visible ventrally, but invisible dorsally), the surface of which lacks periosteal lining.

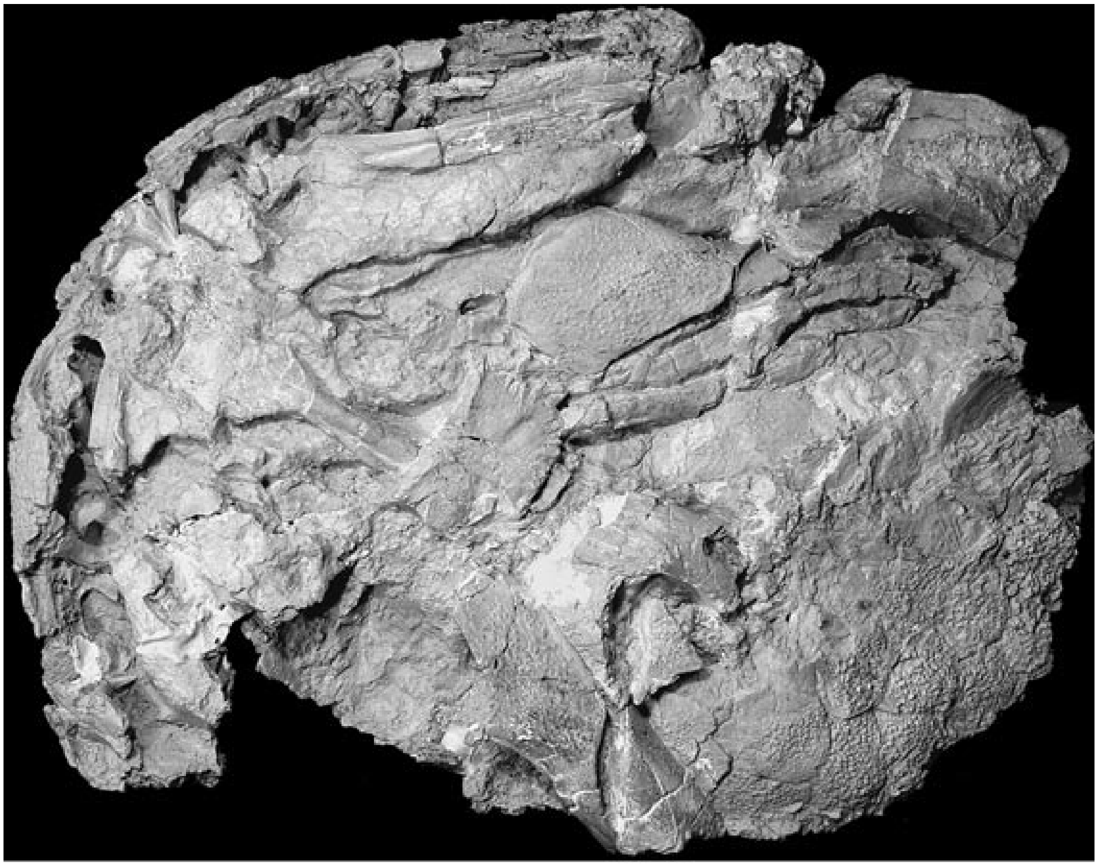
The anterior region of the copula (Figs. 2, 3, *p. ant. Co*) is substantially thicker than its posterior region, abruptly separated from the latter by an almost vertical, straight projection at the midlength of the articular facets for hypobranchials I. In accord with this, the articular facets of the hypobranchials of the first arch (Fig. 2, *ar. art. Hbr I*) are higher and more rounded in outlines than the low, broadly elliptical articular facets of the hypobranchials of the second and third arches. Apparently, the projection separating the high anterior region of the copula did not form a depression or pocket, which is present in *Eusthenopteron* (Jarvik, 1954, text-fig. 9C) and *Medoevia* (Lebedev, 1995, text-fig. 18B). This projection closely adjoined and was articulated with the anterior end of the urohyal (Figs. 2, 3).

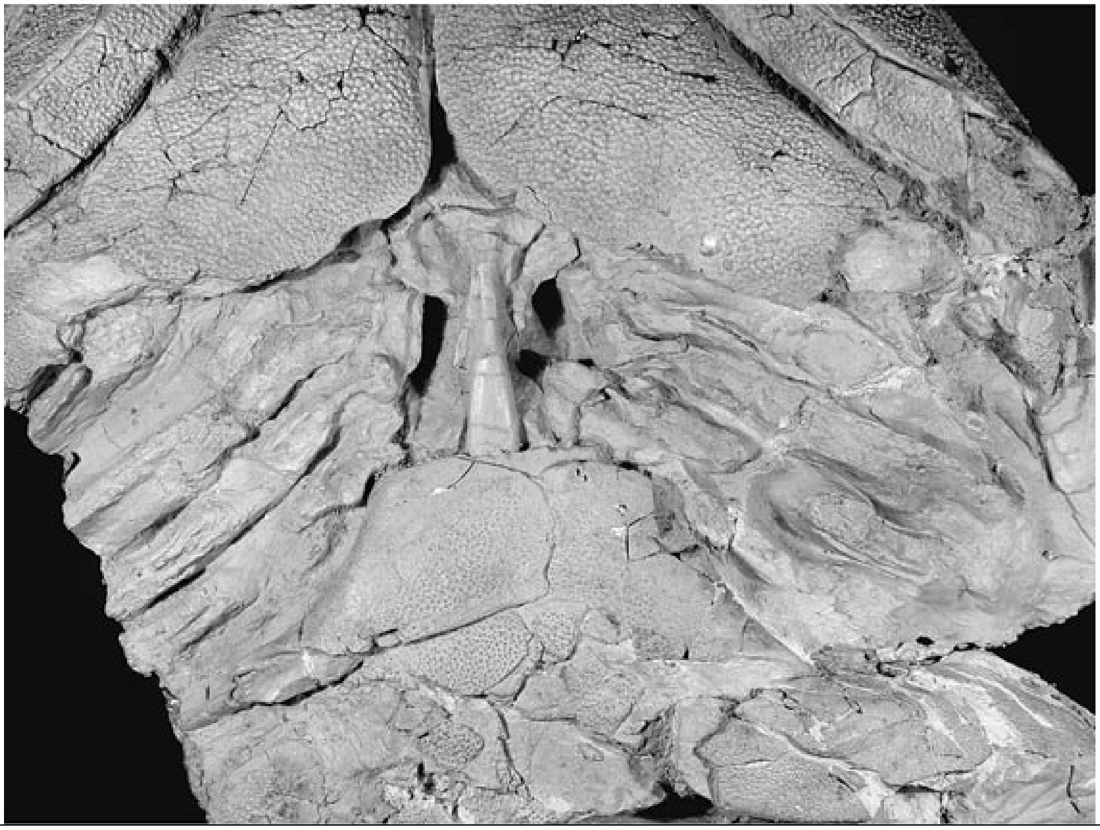
The hypohyalia (Figs. 1–3, *Hh*) are subtriangular in outline in both lateral and medial views; in the natural position, they were vertical relative to the bottom of the oral cavity. The distal ends of the hypohyals are articulated with the anterior edge of the copula on each side of the lingual process. The dorsal side of the left hypohyal (specimen PIN, no. 3547/12, Fig. 1) has a deep fossa extending over most of the bone length. This probably suggests the preservation of a cartilage in the inner region of the hypohyals of *Laccognathus*. The medial surface of the left hypohyal of specimen PIN,

Explanation of Plate 9

Figs. 1 and 2. *Laccognathus panderi* Gross; Latvia, Lode locality; Middle Devonian, Givetian Stage, Gauja Horizon, Lode Formation: (1) specimen PIN, no. 3547/12, hyobranchial skeleton, dorsal view, ×0.55; (2) specimen PIN, no. 3547/8, hyobranchial skeleton, ventral view, ×1.

Plate 10





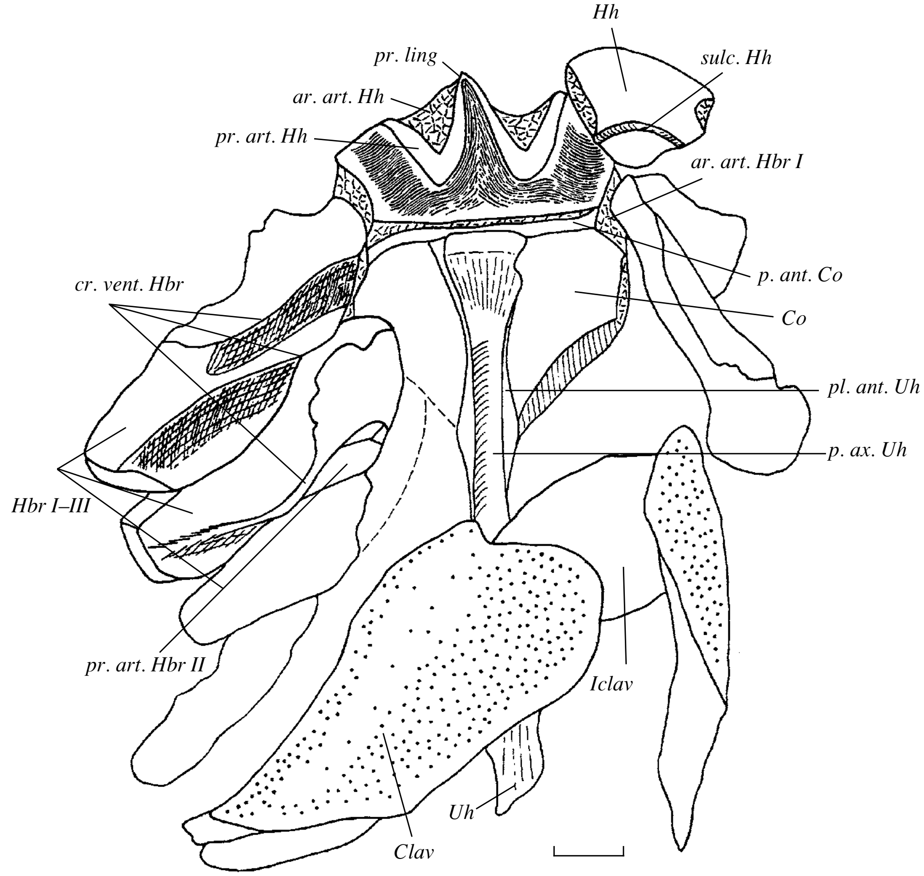


Fig. 2. *Laccognathus panderi* Gross, specimen PIN, no. 3547/8, ventral region of the hyobranchial skeleton, ventral view. Designations: (*ar. art. Hbr I*) articular area for hypobranchial I, (*ar. art. Hh*) articular area for the hypohyal, (*cr. vent. Hbr*) ventral crests on the hypobranchials, (*p. ant. Co*) high anterior region of the copula, (*p. ax. Uh*) ventral rod of the urohyal, (*pr. art. Hbr II*) articular process of hypobranchiale II for connection with hypobranchiale III, (*pr. art. Hh*) articular projection of the copula for the hypohyal, and (*sulc. Hh*) groove for the afferent hyoid artery. For other designations, see Fig. 1. Scale bar, 1 cm.

no. 3547/8 has a relatively deep arched sulcus located close to the posterior margin (Fig. 2, *sulc. Hh*); exactly the same sulcus is observed in this position in *Medoevia lata* (Lebedev, 1995, text-fig. 17H); this is probably a trace of the afferent hyoid artery.

The ceratohyale (Figs. 1, 3, *Ch*) is in the shape of a broad plate with a straight anterior margin and an arched posterior margin; the greatest width is approximately at one-third of the bone length. The presence of depressions without periosteal lining at the proximal and distal ends suggests the preservation of cartilaginous epiphyses of the ceratohyal. A riblike thickening extends along the anterior margin of the bone (Figs. 1, 3, *p. arc. Ch*); it is particularly clearly differentiated on the dorsal side (specimens PIN, nos. 3547/12, 22), but, sometimes, it is also distinct on the ventral surface (PIN, no. 3547/24, Pl. 10, fig. 1). It is approximately one-third as wide as the greatest bone width and expands somewhat near the distal end of the ceratohyal. A deep sulcus extends along the entire anterior margin of the ceratohyal, and, hence, along the riblike thickening (Figs. 1, 3, *sulc. Ch*) and divides the anterior region of the ceratohyal into the dorsal and ventral plates; over the entire extent, the dorsal plate projects anteriorly beyond the edge of the ventral plate and overhangs it. Near the proximal end of the ceratohyal, the dorsal and ventral plates curve somewhat dorsally and ventrally, respectively; thus, the sulcus expands to form an area facing anteriorly (Fig. 3). The proximal region of the ventral plate corresponds to “the lateral crest of the ceratohyale of *Eusthenopteron*,” as was described by Jarvik (1963, text-figs. 16C, 19C). The surface of the thickening that faces inside the oral cavity is covered with small (0.25–0.50, infrequently, up to 1 mm), flat-

Explanation of Plate 10

Figs. 1 and 2. *Laccognathus panderi* Gross, the same locality and age: (1) PIN, no. 3547/24, skeleton of the head, ventral view, ×0.6; (2) PIN, no. 3547/7, skeleton of the head, ventral view, ×0.45.

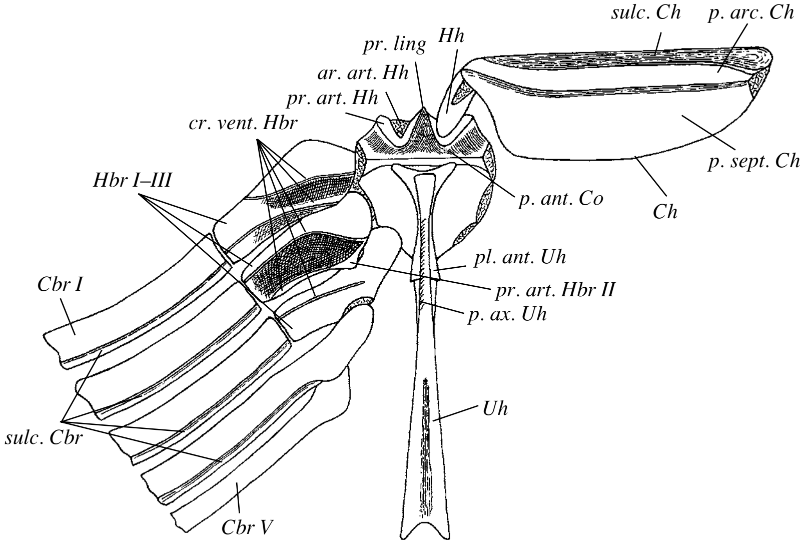


Fig. 3. Reconstruction of the hyobranchial skeleton of *Laccognathus panderi* Gross, ventral view. Designations: (*sulc. Cbr*) groove in the ceratobranchials containing the bases of gill lamellae and branchial septa. For other designations, see Figs. 1 and 2.

tened, triangular denticles (Fig. 1, *dent. Ch*) of the same type as denticles located on the posterior area of the overlapped surface of scales of *Laccognathus* and other porolepiforms (i.e., denticles of the first generation after Ørvig, 1957). The denticles are widely spaced, becoming scattered more densely only along the anterior margin of the dorsal plate of the longitudinal projection. There are no sutures or other traces of individual dental plates; thus, an impression is formed that the denticles are directly attached to the surface of the perichondral ossification of the ceratohyal. In specimen PIN, no. 3547/12, the internal surface of the right ceratohyal has relatively shallow tortuous grooves (Fig. 1, *sulc. ves.*) posterior to the longitudinal thickening; similar grooves are also observed on the dorsal side of the ceratohyal of *Medoevia lata* (Lebedev, 1995, text-fig. 17A); they are probably imprints of blood vessels associated with the hyoid hemibranch.

The longitudinal riblike thickening can be treated as follows. Apparently, in the ancestors of crossopterygians, the ceratohyal, like the branchial arches, was initially composed of an ossifying visceral arch and a branchial septum continuing it externally (in *Latimeria*, the branchial septa are well developed, see Millot et al., 1978, pp. 29, 30, text-fig. 7). The participation of the hyoid arch in the support of the operculogular membrane required changes in the shape of its ventral segment, which was transformed into a wide plate (a more or less expanded ceratohyal is characteristic of all Osteichthyes and is particularly well-pronounced in crossopterygians). This was achieved by the addition of the ossifying branchial septum of the future hyoid arch to the proper visceral bone. Thus, the longitudinal riblike projection with denticles is the arched region of the primary ceratohyal, while the plate with imprints of blood vessels, which continues it posterolaterally, is its septal region. If this is the case, Porolepiformes are the only osteichthyan group that retains the traces of the initial double structure of the ceratohyal. Osteolepiforms, in particular, *Medoevia*, have nothing comparable to the riblike thickening of *Laccognathus*, and the internal surface of their ceratohyal is even.

Laccognathus has five branchial arches, the distal ends of which are closely spaced. Only three anterior branchial arches are directly articulated with the copula; arch IV is articulated with hypobranchial III, while arch V is articulated with the distal end of arch IV. The epibranchials (as well as fragmentary hyomandibulars) are present in the material examined; however, they are not described here because of poor preservation and little significance for subsequent discussion.

Hypobranchials I–III (Figs. 1–3, *Hbr*) are relatively short and wide, located in the same plane as the copula. Hypobranchials I and III are distinguished by the curved shape, so that the convex side of the bend of the first hypobranchial is directed anteriorly, while that of the third hypobranchial is directed posteriorly. The posteromedial projection formed by this bend of hypobranchial III provides attachment for the distal end of the fourth branchial arch (Figs. 1, 3). The dorsal surface of the hypobranchials is flat, while the ventral surface has longitudinal crests up to 5 mm high, which probably form attachment areas for the ventral branchial muscles (mm. interarcuales ventrales); the hypobranchial of the first arch has two crests of this kind (Figs. 2, 3, *cr. vent. Hbr*). Hypobranchialia II and III are connected to one another by ventral processes (Figs. 2, 3, *pr. art. Hbr II*), as in *Glyptolepis groenlandica* (Jarvik, 1963, 1972). The distal ends of the three anterior hypobranchials closely adjoin each other, and their contacts with the lateral margins of the copula are wide and tight. These features suggest that the articulation between the copula and the distal regions of the branchial arches (in contrast to that of the hyoid arch) was of rather low mobility. The articulation between hypobranchials II and III compensated the absence of connections between the copula and two posterior arches; this indicates that synchronism in movements of the ventral regions of the anterior and posterior arches in the vertical plane was of great importance for Porolepiformes.

Ceratobranchialia I–IV (Figs. 1, 3, *Cbr*) are long, flattened, slightly arched elements. Their posterior (external) margin has a groove (Fig. 3, *sulc. Cbr*), which noticeably divides the posterior region of the bone into the dorsal and ventral plates. This groove contained the bases of gill lamellae and branchial septa. Ceratobranchial V is thinner and shorter than the others and lacks a groove on the posterior margin. Distally, the ceratobranchials of three anterior branchial arches are articulated with respective hypobranchials, while ceratobranchials IV and V are connected to the posterior margin of the hypobranchial of the third arch and the distal area of ceratobranchial IV, respectively. The fourth and fifth branchial arches of *Laccognathus* apparently lacked separate hypobranchials, as is in general characteristic of Osteichthyes.

Urohyale (Figs. 1–4, *Uh*) is an anteroposteriorly extended and dorsoventrally flattened bone. It consists of two major components, a cylindrical rod positioned ventrally (Figs. 2, 3, *p. ax. Uh*) and a horizontal plate overlying it dorsally (Figs. 1–4, *pl. ant. Uh* and *pl. post. Uh*). The two components are not separate over the entire extent of the bone, i.e., the boundary between them is indiscernible near the anterior end of the urohyal and within the posterior third of the urohyal. In large individuals, the rod-shaped region of the urohyal is clearly isolated from the platelike region within a smaller extent than in smaller individuals. The two components are best pronounced in specimen PIN, no. 3547/8. The anterior margin of the urohyal is fan-shaped (Figs. 3, 4a); in the specimens with natural bone arrangement (PIN, nos. 3547/8, 24), it rests against the posterior margin of the high anterior region of the copula and lies at the same level as its ventral surface. The urohyal was probably connected to the copula by tendons.

The dorsal platelike component of the bone is divided into two parts by a sharp constriction; the anterior part (Figs. 1–4, *pl. ant. Uh*) is approximately one-third of the total urohyal length. Jarvik (1963, text-fig. 16A) designated this part of the urohyal of *Glyptolepis groenlandica* at the point of constriction as “wing-like projection.” On the dorsal side, it is separated from the posterior part of the dorsal plate by a border in the shape of a blunt angle, with its apex turned anteriorly (Fig. 1, specimen PIN, no. 3547/12). Posterior to this boundary, the bone surface is positioned substantially lower than in the anterior part. The central region of the dorsal surface of the posterior part of the dorsal plate of the urohyal (Figs. 1, 4a, *pl. post. Uh*) is occupied by a wide medial groove (Figs. 1, 4a, *ar. m. sth.*), which is bordered laterally by the flanges of rising margins of the bone. This groove corresponds in the position on the dorsal side of the urohyal to concave areas for the sternohyoideus muscle of *Latimeria* (Fig. 4b, *ar. m. sth.*), but differs in the fact that it is unpaired. The anterior part of the dorsal plate of *Laccognathus* that lies anterior to the groove could have provided attachment for the interarcuales ventrales muscles, as was proposed for the wing-like projection of *Glyptolepis* (Jarvik, 1963, text-fig. 18E). From the constriction, the dorsal plate of the urohyal, along with the attachment area for the sternohyoideus muscle, gradually expands posteriorly. Using available material, it is impossible to reconstruct the caudal extent of the bone or the shape of its posterior end; however, it is evident that the urohyal extended caudally beyond the articulation between the clavicles and the interclavicle (Figs. 1, 2).

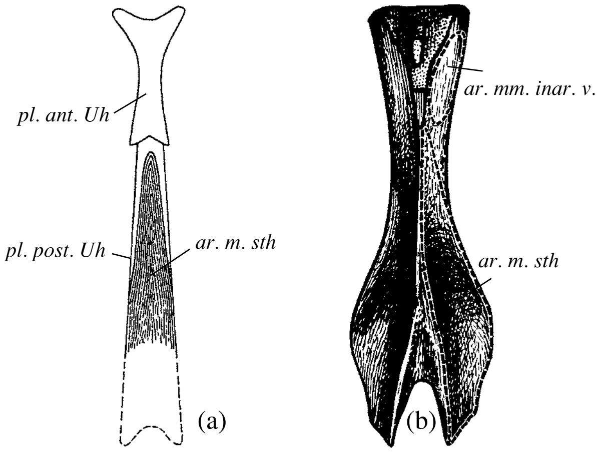


Fig. 4. Urohyal, dorsal view in (a) *Laccognathus panderi* Gross and (b) *Latimeria chalumnae* Smith (after Millot and Anthony, 1958, text-fig. 15). Designations: (*ar. mm. inar. v.*) attachment area of the common base of the interarcuales ventrales muscles. For other designations, see Fig. 1.

The above description shows that the general pattern of the hyobranchial skeleton of *Laccognathus panderi* is rather similar to that of *Glyptolepis groenlandica* (Jarvik, 1963, 1972). However, certain minor differences deserve mentioning. The high anterior region of the copula of *Laccognathus* is substantially shorter than in *Glyptolepis*; it is shorter than half of the greatest width of the copula (data on three specimen, PIN, nos. 3547/8, 24, 26), whereas that of *G. groenlandica* is somewhat longer (Jarvik, 1972, pl. 18, fig. 1; pl. 22, fig. 2); in addition, its posterior boundary (projection) passes in *Glyptolepis* posterior to the articular facets for hypobranchials I (Jarvik, 1972, pl. 22, figs. 2, 5) rather than in the middle of their extent (as in *Laccognathus*). In *Glyptolepis*, the articular facets for the hypohyals face mostly anteriorly and only slightly come onto the ventral side of the copula (Jarvik, 1972, pl. 22, figs. 2, 4, 5). Finally, the posterior region of the urohyal of *Lac-*

cognathus expands to a much greater extent than in *Glyptolepis*.

The total number of branchial arches in rhipidistians should also be discussed. The fact that Jarvik (1963, text-fig. 16A; 1972, text-fig. 29A; 1980, text-fig. 199) figured only four branchial arches in the reconstruction of the hyobranchial skeleton of *Glyptolepis groenlandica* was based on a specimen (Jarvik, 1972, pl. 18, fig. 1) that undoubtedly underwent a postmortem loss or disruption of posterior arches. In *Medoevia*, all ceratobranchials are disrupted, so that it is impossible to determine whether or not it had the fifth branchial arch. It is also impossible to arrive at an unequivocal conclusion on this question in *Mandageria* because of poor preservation of its branchial skeleton (Johanson and Ahlberg, 1997, text-fig. 13). Thus, specimen PIN, no. 3547/12 of *Laccognathus panderi* is presently the only case of the presence of five branchial arches in rhipidistians. At the same time, there are no unequivocal data on a decrease in the number of branchial arches in other members of this group.

Medoevia lata Lebedev, 1995

A detailed morphological description and figures of skeletal elements of *Medoevia* were provided by Lebedev (1995). In the present study, only the basic structural characters of the hyobranchial skeleton of this fish that are important for further discussion are described.

The basibranchial series is represented by two elements, i.e., the anterior and posterior copulae. The anterior copula is a large expanded bone rounded multiangular in outlines. It is articulated with the hyoid arch and the first two branchial arches. The articular facets for the hypohyals are on the anterior side of the copula, those for hypobranchials I and II are on the lateral sides. The facets for hypobranchials II closely adjoin each other, while the facets for the hypohyal and hypobranchials I are separated by a significant distance. Like the single copula of *Laccognathus* or *Latimeria*, the anterior copula of *Medoevia* is divided into a high anterior region and a low posterior region. In *Medoevia*, the boundary between them (a transverse projection on the ventral side of the bone) is in line with the midlength of the articular facets for hypobranchials I, as in *Laccognathus* and distinct from *Glyptolepis* (see above). The ventral surface of the high anterior region of copula I has two symmetrically positioned facets lacking periosteal lining. They are located just posterior to the hypohyal articular facets, but do not continue them; apparently, they provided attachment for the tendons stretching from the anterior end of the urohyal. At the boundary between the high anterior region and the low posterior region of copula I, there is the basibranchial fossa, which is continued anterodorsally inside the bone by a regularly cone-shaped cavity. This cavity is blind, does not form a basibranchial canal, which was described in *Eusthenopteron* (Jarvik, 1954, 1963). The posterior copula is a small bone triangular in horizontal projection, which closely adjoins anteriorly the posterior margin of copula I. The posterior copula is connected to the third pair of branchial arches.

The hypohyalia are positioned in the vertical plane, triangular in medial and lateral views, articulated with the anterior copula. The ceratohyals are large platelike bones with a straight anterior edge and arched posterior edge, a deep groove along the anterior margin, and imprints of blood vessels on the dorsal side, as in *Laccognathus*; however, *Medoevia* lacks a trace of a detached arched part of the ceratohyal. Hypobranchials I–III closely approach their counterparts distally, but do not come in contact by their anterior or posterior margins, nor form articulations, in contrast to those of Porolepiformes. As in *Laccognathus* and *Glyptolepis*, hypobranchial III forms a blunt angle (with its distal part oriented anteromedially, and the proximal part directed laterally and slightly posterolaterally) and has a small projection without periosteal lining in the middle of the caudomedial margin, which provided attachment for the fourth branchial arch.

The urohyale is a vertical, laterally compressed plate with a widened anterior end. The lateral surface of the bone has an oblique crest that extends anteroventrally and divides it into anterodorsal and posteroventral areas, which are approximately equal in size. It differs from the urohyal of *Eusthenopteron* (Jarvik, 1954, text-fig. 10; 1963, text-fig. 16D) in the lower posterior region of the bone and the equal size of the lateral areas (in *Eusthenopteron*, the posteroventral area is substantially larger than the anterodorsal area). The presumed sublingual rod of *Medoevia* (Lebedev, 1995, text-fig. 18A) is too poorly preserved (probably because of incomplete ossification) to compare it with that of *Eusthenopteron*.

RECONSTRUCTION OF THE HYPOBRANCHIAL MUSCLES

Jarvik (1963) reconstructed the hypobranchial musculature of *Eusthenopteron* in the following way. The anterior hypobranchial muscles are paired geniohyoideus muscles and the “hyogenioglossus” muscle (hypothetical predecessor of the genioglossus and hyoglossus muscles of tetrapods), which originate from the mandibular symphysis and extend caudally along the ventral and dorsal sides of the sublingual rod, respectively. The geniohyoideus muscle is located ventral to the anterior basibranchial, while the “hyogenioglossus” muscle passes through the anterior part of this bone along the basibranchial canal. Both muscles are inserted in the lateral surface of the vertical plate of the urohyal below the lateral crest. The posterior pair of the hypobranchial muscles is the sternohyoideus (= rectus cervicis) muscle, which originates from the pectoral girdle and hypaxial pectoral musculature and is inserted in the lateral surface of the urohyal above the lateral crest.

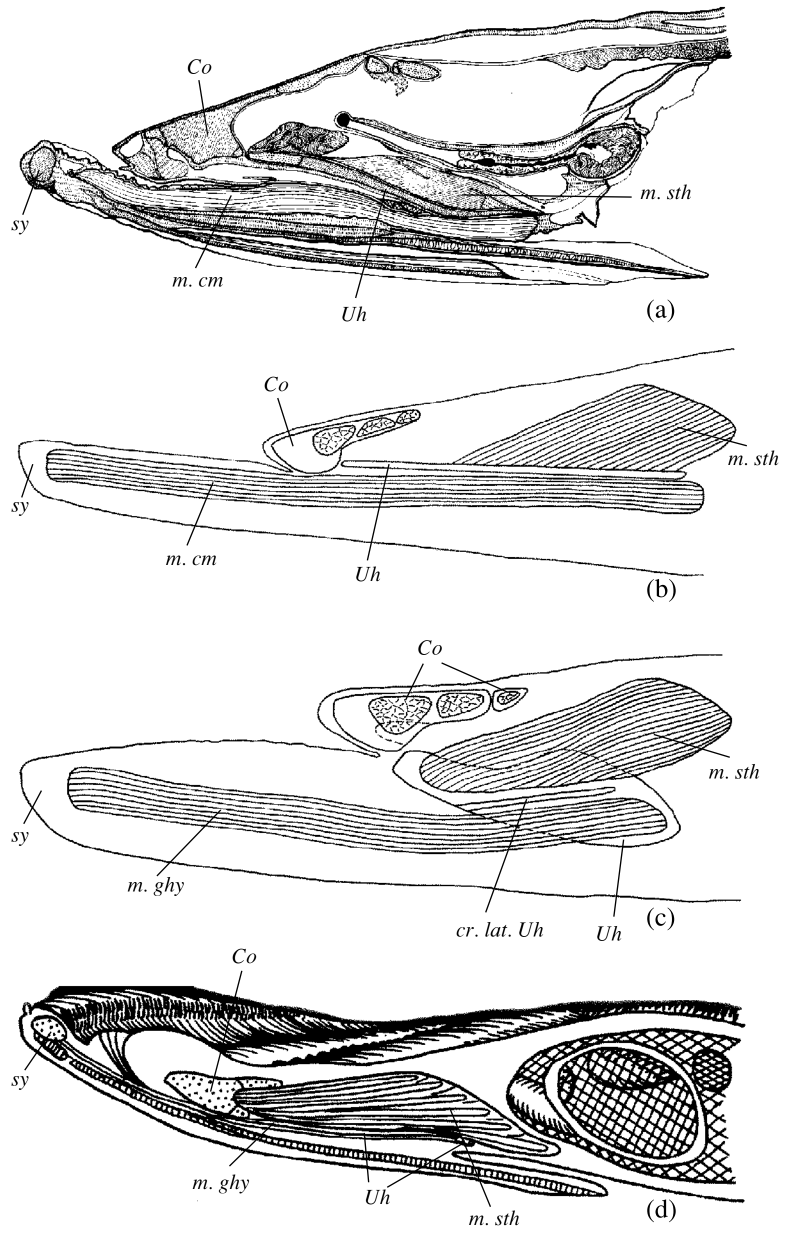


Fig. 5. Sagittal section through the lower jaw and the bottom of the buccopharyngeal cavity (a, d); schematic reconstruction of hypobranchial muscles, side lateral view (b, c); (a) *Latimeria chalumnae* Smith (after Millot and Anthony, 1958, pl. III); (b) *Laccognathus panderi* Gross; and (c) *Medoevia lata* Lebedev; (d) larval *Ranodon sibiricus* Kessler (after Severtsov, 1968, text-fig. 1). Designations: (*cr. lat. Uh*) lateral crest on the urohyal, (*m. cm*) coracomandibularis muscle, (*m. ghy*) geniohyoideus muscle, (*m. sth*) sternohyoideus muscle, and (*sy*) symphysis of the lower jaw. For other designations, see Fig. 1.

But for the existence and position of the "hyogenioglossus" muscle (as is evident from the above description, *Medoevia* lacks a basibranchial canal), I agree with this reconstruction of the hypobranchial muscles of Osteolepiformes. However, it should be noted that, among the extant Gnathostomata, only larval caudate amphibians display a similar arrangement of muscles. They are unique in that the anterior hypobranchial (geniohyoideus) muscle is inserted by its posterior end in the urohyal from below (usually in the posterior expansion of the urohyal, the cartilago triangularis, which ossifies in adults to form the triquetrum bone) (Fig. 5d, *m. ghy, Uh*). In *Proteus anguineus*, it is inserted in the entire lower surface of the urohyal (Severtsov, 1968). In primitive actinopterygians, such as *Polypterus, Amia*, and Acipenseriformes, the corresponding muscle (m. branchiomandibularis) is inserted by the posterior end in the hypobranchial of the third branchial arch. In Teleostei, it is absent (the so-called geniohyoideus muscle of Teleostei is a visceral muscle, derived from the ventral parts of the mandibular and hyoid constrictors, see Winterbottom, 1974), whereas *Latimeria*, dipnoans, and elasmobranchians have a coracomandibularis (= geniothoracicus) muscle, which connects the mandibular symphysis to the pectoral girdle (Fig. 5a, *m. cm*). The geniohyoideus muscle of tetrapods is inserted by its posterior end in the hypoglossal skeleton, while only caudate amphibians display a structure corresponding to the urohyal of crossopterygians. The homology of the pedicle of the copula of larval caudates and the urohyal is supported not only by its embryonic development (produced by the endomesoderm, in contrast to the copula itself, which is formed by the ectomesenchyme of the neural crest, as the entire visceral skeleton, see Jarvik, 1954, 1963) but also by the arrangement of fibers of the sternohyoideus muscle. The major portion of this muscle (pars profundus) passes above the pedicle of the copula and is inserted in the dorsal side of the copula and adjacent hypobranchials of the second arch (Fig. 5d, *m. sth.*). In fish, this muscle never passes dorsal to the basibranchials; however, its fibers are inserted in the dorsal side of the urohyal in both *Latimeria* (Millot and Anthony, 1958) and Teleostei (Winterbottom, 1974). The most credible treatment of the condition observed in larval caudates is to take the pedicle of the copula for a transformed urohyal, the dorsal side of which had insertion area for the sternohyoideus muscle in their ancestors. Subsequently, as the urohyal fused with the copula, fibers of this muscle were displaced anteriorly, onto the dorsal surface of the true copula.

Thus, the hypobranchial muscles of Osteolepiformes, with the sternohyoideus muscle inserted in the dorsal region of the urohyal and the posterior end of the geniohyoideus muscle inserted in the ventral region of this bone (Fig. 5c), should be reconstructed based only on analogy with the condition observed in caudates (Fig. 5d). It is shown below that this reconstruction receives additional support from the general trend in phylogenetic changes of the urohyal and hypobranchial muscles in crossopterygians. Here, it is necessary to consider the arrangement of these muscles in Porolepiformes, which was not discussed by Jarvik.

The urohyal of *Laccognathus* is rather similar to that of *Latimeria* in shape and the pattern of attachment to the copula and considerably differs from that of Osteolepiformes. Similar characters of these structures in porolepiforms and coelacanths as well as differences from osteolepiforms are listed below.

In *Latimeria, Laccognathus*, and *Glyptolepis*:

(1) The urohyal is a dorsoventrally flattened plate with attachment areas for muscles on the dorsal surface (Fig. 4).

(2) The anterior end of the urohyal is dorsoventrally flattened, located at the same level as the ventral surface of the anterior part of the copula, and attached to the projection formed by the posterior side of the high anterior region of the copula.

(3) The caudal surface of the high anterior region of the copula forms a steep projection.

In *Eusthenopteron* and *Medoevia*:

(1) The urohyal is a vertical plate with paired attachment areas for muscles on the lateral sides.

(2) The anterior end of the urohyal is high, projects beyond the level of the lower surface of the copula, is attached by a pair of tendons to the ventral surface of the high anterior region of the copula just posterior to the articular facets of the hypohyals (Jarvik, 1954, text-fig. 9C, 11A; Lebedev, 1995, text-fig. 18B).

(3) The caudal surface of the high anterior region of the copula forms a deep cone-shaped fossa (in *Eusthenopteron*, it is continued anteriorly by the basibranchial canal), which probably contained a projection of the thyroid gland (Jarvik, 1963).

The close similarity in the urohyal structure between Porolepiformes and *Latimeria* suggests that the positions of hypobranchial muscles, which are tightly related to this element, were also similar; in particular, porolepiforms had coracomandibularis muscles, which connected the mandibular symphysis to the pectoral girdle (Fig. 5b). Taking into account the presence of this muscle in dipnoans and Elasmobranchii, it is possible to take this condition of the hypobranchial musculature for a primitive state for Sarcopterygii and bony fishes as a whole. The urohyal in the shape of a dorsoventrally flattened plate shows that Porolepiformes and coelacanths have retained this primitive condition. When comparing with the structural pattern of tetrapods, i.e., the insertion of the anterior hypobranchial muscle (a homologue of the coracomandibularis muscle) to the hypoglossal skeleton (in caudates, to the urohyal) and the presence in Osteolepiformes of the urohyal of a basically different structure (in the shape of a high vertical plate with paired attachment facets for muscles on the lateral sides), it is possible to conclude that the change in the shape of the urohyal is a direct consequence of the displacement of the origin of the coracomandibularis muscle from the pectoral girdle onto this bone, that is, its transformation into the geniohyoideus muscle (Figs. 5b, 5c, *m. cm, m. ghy*). Actually, it is clearly seen in a sagittal section of the head of *Latimeria* (Fig. 5a) that the coracomandibular muscle is rather thick, so that a supplementary vertical plate of the urohyal is required for the insertion of its fibers. Evolutionary development of the urohyal in Teleostei provides a good analogy. In the majority of Teleostei, this bone is an expanded horizontal plate with a vertical dorsal crest (Allis, 1903; Winterbottom, 1974; Anker, 1974; original data on *Oncorhynchus* and *Cyprinus*); fibers of the stout sternohyoid muscle are inserted in both the dorsal surface of the horizontal plate and the lateral surfaces of the dorsal crest. In primitive actinopterygians, the urohyal is absent (Acipenseriformes, *Lepisosteus, Amia*, apparently, most of the palaeoniscids and extinct Holostei) or is represented by small bones, which do not provide attachment for all fibers of the sternohyoid muscle (*Polypterus*) (Arratia and Schultze, 1990). Thus, the increase in the area of the urohyal, in particular, the development of the vertical crest at the early stages of Teleostei evolution was connected with the insertion of most of the fibers of the sternohyoid muscle in this bone. Similar events occurred at early stages of the Osteolepiformes evolution, the attachment of fibers of the coracomandibularis muscle to the ventral region of the urohyal caused the development of the vertical plate of this bone. This new condition, with the geniohyoideus muscle connecting the lower jaw with the hyoid apparatus, was inherited by tetrapods, in particular, by caudates from osteolepiforms (Figs. 5c, 5d).

DISCUSSION

The Structure of the Hyobranchial Apparatus and the Diphyletic Origin of Tetrapods

As Jarvik (1963, 1972) derived the pattern of the hyobranchial apparatus of larval caudates from that of Porolepiformes, he paid special attention to the reduction of the ventral regions of posterior branchial arches, which lost direct contact with the copula, and the development of articulations between the distal ends of branchial arches II, III, and IV, which are characteristic of both groups. This was contrasted with the case of *Eusthenopteron*, each of five branchial arches of which came in contact with the basibranchial series independently, while the elements of neighboring arches were not articulated with each other (Jarvik, 1954, 1963). However, new data on the hyobranchial apparatus of Osteolepididae (Lebedev, 1995) and Eusthenopteridae (Johanson and Ahlberg, 1997) have shown that only three anterior branchial arches of osteolepiforms are directly articulated with the basibranchial series, while the distal end of the fourth arch is articulated with hypobranchial III. Based on these new morphological data, particularly those on *Mandageria fairfaxi*, which is closely related to *Eusthenopteron*, Johanson and Ahlberg (1997) concluded that Jarvik's interpretation of the branchial skeleton of *Eusthenopteron* and his idea that the above described pattern of the hyobranchial apparatus was uniform in all Sarcopterygii were in error. If this is the case, larval caudates could have inherited the pattern of the hyobranchial skeleton from either Porolepiformes or Osteolepiformes. At the same time, taking into account our conclusions about the arrangement of hypobranchial muscles in these two crossopterygian groups, porolepiforms should be excluded from potential ancestors of caudates.

Another reason for placing caudates close to Porolepiformes was the presence in the latter of musculus subarcualis rectus I and musculus branchiohyoideus externus (in extant taxa, it is only present in larval caudates), which were reconstructed by Jarvik based only on the presence of imprints treated as scars of these muscles on the external surface of the ceratohyal of *Glyptolepis*. This condition was opposed to the case of *Eusthenopteron*, a large area of the external surface of the ceratohyal of which was occupied by dental plates (Jarvik, 1963, 1972). In larval caudates, these muscles connect the external surface of the ceratohyal to the first branchial arch, closing the first branchial cleft; the subarcualis rectus muscle is located near the midline of the body and connects the distal regions of arches, while the branchiohyoideus externus muscle extends through most of the ventral surface of the ceratohyal and reaches the proximal end of ceratobranchial I (Severtsov, 1968). This situation is impossible in the case of fish possessing a gill cover (operculum), including crossopterygians, because the ceratohyal is a supporting structure for the operculogular membrane, so that all muscular fibers originating from its external surface extend inside the operculum and cannot be inserted in the first branchial arch. Thus, the reconstruction of visceral muscles of *Glyptolepis* proposed by Jarvik (1963, text-fig. 18E; 1972, text-fig. 101B; 1980, text-fig. 199) is highly improbable. The positions of the subarcualis rectus I and branchiohyoideus externus muscles characteristic of caudates could have developed only in animals that had already lost internal gills and operculum; thus, they do not provide evidence for particular ancestors of caudates among fishes.

Urohyale

Among extant groups, the urohyal is present in the majority Teleostei and *Latimeria* (about caudates, see above). The urohyal of Teleostei is a membrane bone developing in the tendon of the sternohyoideus muscle (Arratia and Schultze, 1990). The same is true of three small bones that occupy a similar position in *Polypterus*. Of extant actinopterygians, only siluroids have a cartilage that originates from the basibranchial region and participates secondarily in the formation of the anterior end of the urohyal (Arratia and Schultze, 1990). At the same time, the anterior end of the urohyal of *Latimeria* has a cartilaginous epiphysis, which connects this bone to the copula; a roentgenographic study has shown that this epiphysis continues the axial part of the urohyal, which differs in histology from the peripheral region of the bone (Millot and Anthony, 1958, p. 57). Millot and Anthony concluded that the urohyal of *Latimeria* is a dual formation composed of an endochondrally ossifying rod and an enveloping bony cover of membrane origin. Our data on the urohyal of *Laccognathus* agree with this interpretation. The ventral rod corresponds to the axial endochondral part of the urohyal of *Latimeria*, while the dorsal plate is probably a membrane bone. This bone develops on the dorsal surface of the primary cartilaginous urohyal, that is, in the region where muscles are inserted, and consists of two parts, the posterior of which is approximately three times as long as the anterior part; this exactly corresponds to the positions and relative lengths of the interarcuales ventrales and sternohyoideus muscles in *Latimeria* (Fig. 4). This is additional evidence that the shape of the urohyal depends on the pattern of muscles attachment, which influences the development of membrane bones. In coelacanths and porolepiforms, these bones transformed the initial cartilaginous rod into a horizontal plate, whereas, in Osteolepiformes (if they also had a rod-shaped rudiment of the urohyal, as was proposed by Millot and Anthony), the urohyal was in the shape of a vertical plate. The fact that, in large individuals of *Laccognathus*, the rod-shaped part of the urohyal is detached to a lesser extent suggest that the membrane component of the bone increased with age.

As was shown above, the urohyal of Porolepiformes and Osteolepiformes, as that of *Latimeria*, is connected to the copula, namely, to its part that, judging from the order of articulation of visceral arches, corresponds to the basihyal (in Osteolepiformes) or, possibly, basibranchial I (in Porolepiformes and Coelacanthiformes). At the same time, the urohyal of Teleostei is always connected to the hypohyals (Winterbottom, 1974); the tendons of the sternohyoideus muscle are also connected to the hypohyals in the lower Actinopterygii, such as *Polypterus*, Acipenseriformes, *Lepisosteus*, and *Amia* (Allis, 1922; Lauder, 1980b; Arratia and Schultze, 1990). Taking into account the presence of the urohyal connected to the ventral projection of the anterior region of the "basibranchiohyale" in the Devonian dipnoan *Griphognathus whitei*, (Miles, 1977, p. 272, text-fig. 138), it is possible to propose that the place of insertion of the sternohyoideus muscle in the visceral skeleton is a character that marks the divergence between Sarcopterygii and Actinopterygii. In sarcopterygians, this muscle is inserted in the basihyal (through the urohyal), while that of actinopterygians is inserted in the hypohyals.

Functional Significance of Evolutionary Changes in the Hypobranchial Musculature

The transformation of the coracomandibularis muscle into the geniohyoideus muscle, which occurred at the early stage of the Osteolepiformes evolution, probably marked a functional change in the hyobranchial apparatus of this group. It is possible to recognize the significance of this event based on the functions of these muscles in extant taxa. The coracomandibularis muscle, which is present in Elasmobranchii, Dipnoi, and *Latimeria*, is traditionally treated as a depressor of the lower jaw (Millot and Anthony, 1958, p. 60) based on the arrangement of its fibers, which originate from the pectoral girdle and are inserted in the mandibular symphysis. Subsequently, experimental data showed that, in *Latimeria* and extant Dipnoi, this muscle does not participate in lowering the lower jaw (Lauder, 1980a; Bemis and Lauder, 1986). However, this conclusion cannot mechanically be extended to rhipidistians and common ancestors of sarcopterygians. The basic argument against this function of the coracomandibular muscle in *Latimeria* is the fact that, as its lower jaw is abducted, the distance between the symphysial region and the pectoral girdle increases rather than decreases, i.e., the coracomandibularis muscle extends rather than constricts. This pattern of movements in *Latimeria* is connected with the correlation between the lowering of the lower jaw and raising of the ethmosphenoid skull region along with the palatoquadrate complex, which causes an anterior displacement of the quadrate–mandibular articulations (Thomson, 1969; Lauder, 1980a). This correlation is provided by the pattern of double suspension of the lower jaw (unique to coelacanths), which is supported by both the true jaw articulation and, through the retroarticular process and symplecticum, by the hyoid arch. As rhipidistians lack such a double connection and the lower jaw is lowered independently of movements of the palatoquadratum (Thomson, 1969), the region of the coracomandibularis muscle did not extend when they opened the mouth. In Dipnoi, the hyoid constrictor gave rise to a special muscle, the depressor mandibulae (= retractor mandibulae), which functioned as the basic depressor of the lower jaw (Fox, 1965; Bemis and Lauder, 1986). The development of this muscle in dipnoans was probably connected with a general reduction of the operculum, which had much in common with the development of a similar depressor of the lower jaw in tetrapods. In any event, there is no reason to presume the presence of this muscle in rhipidistians. Thus, the reasons that contradict the participation of the coracomandibularis muscle in lowering the mandible in extant coelacanths and dipnoans are insignificant for common ancestors of Porolepiformes and Osteolepiformes. Moreover, the coracomandibular muscle undoubtedly functions as a depressor of the lower jaw in Elasmobranchii (Gimmel'reich, 1952; Moss, 1972); thus, this function of the coracomandibularis muscle is probably primary in all Gnathostomata.

The geniohyoideus muscle of tetrapods, as the muscles occupying a similar position (longitudinal fibrous muscles connecting the lower jaw to the hypoglossal skeleton), i.e., the branchiomandibularis muscle of the lower actinopterygians and the protractor hyoidei (= "geniohyoideus") muscle of Teleostei, protracts the hyoid apparatus, functioning as an antagonist of the sternohyoideus muscle (Severtsov, 1968; Anker, 1974; Lauder, 1980b). As the sternohypoglossal muscle displaces the hyobranchial skeleton ventrocaudally and, hence, lowers the bottom of the buccopharyngeal cavity, the geniohyoideus muscle, working in opposite direction, promotes the elevation of the bottom of the buccopharyngeal cavity. Thus, the transformation of

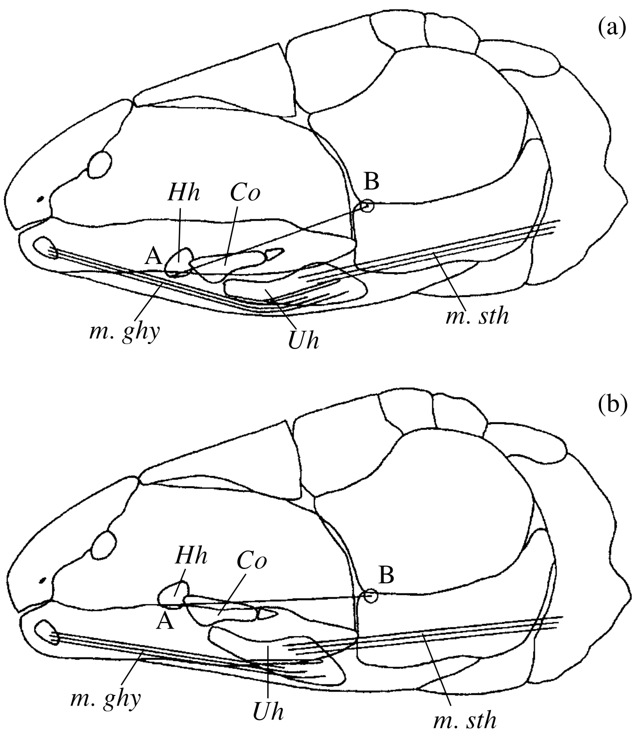


Fig. 6. Movements of the copula in *Medoevia lata*: (a) sternohyoideus muscle is constricted and (b) geniohyoideus muscle is constricted. For designations, see Figs. 1 and 5; for explanation, see the text.

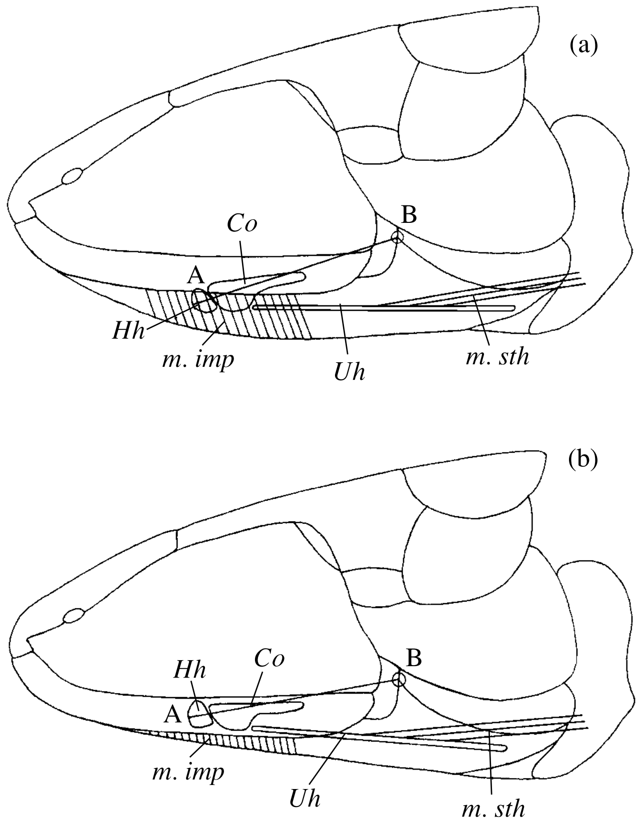


Fig. 7. Movements of the copula in *Laccognathus panderi*: (a) sternohyoideus muscle is constricted and (b) intermandibularis posterior muscle is constricted. Designations: (*m. imp*) intermandibularis posterior muscle. For other designations, see Figs. 1 and 5; for explanation, see the text.

the coracomandibularis muscle into the geniohyoideus muscle reflects the change in functions of this muscle from lowering the lower jaw to protraction of the hyobranchial apparatus. In this case, the role of a mandibular depressor apparently passed in Osteolepiformes to the sternohyoideus muscle, the effect of which is transferred to the lower jaw from the hyobranchial skeleton through the mandibulohyoid tendon, as in all extant Actinopterygii (Lauder, 1980b). However, early osteolepiforms already had muscles that provided protraction of the hyobranchial skeleton. These are transversely striated muscles, derivatives of the superficial constrictors of the jaw and hyoid arches (intermandibularis posterior and interhyoideus muscles). They are present in amphibians, dipnoans, *Latimeria*, and primitive actinopterygians (*Polypterus, Amia*, etc.); in all the groups listed, they show the same structure (Millot and Anthony, 1958; Fox, 1965; Lauder, 1980b) and similar function, which is a decrease in the volume of the buccopharyngeal cavity by raising its bottom (Severtsov, 1968, 1971, 1972; Lauder, 1980b). The presence of these muscles in extant groups suggests that their structure and functions were formed in common ancestors of Osteichthyes or even in early Gnathostomata. The question arises as to what the reason was for the formation of two additional muscles in osteolepiforms that protracted the hyobranchial apparatus. Apparently, the major functional innovation provided by the geniohyoid muscle was an increased range of movements of the anterior region of the copula in the vertical plane. As is well known, the copula supports the tongue of fishes; in many of them, in particular, in all crossopterygians, it has dental plates (Jarvik, 1954, 1972; Millot and Anthony, 1958). Certainly, it is important to control movements of this structure, particularly in order to manipulate small prey in the mouth cavity. Figure 6 shows the movements of the copula by the geniohyoideus and sternohyoideus muscles, using the example of *Medoevia*. Constriction of the geniohyoideus muscle causes rotation of the lever arm AB (ceratohyale) around the immobile axis B (articulation between the interhyale and the hyomandibulare). The geniohyoid muscle is inserted (in the posteroventral area of the lateral surface of the urohyal) at some distance from the anterior region of copula I; therefore, as this muscle is constricted, the urohyal pushes out copula I, which rises above the bottom of the mouth cavity (Fig. 6b). For comparison purposes, Fig. 7 shows movements of the copula caused by the intermandibularis posterior muscle (using *Laccognathus* as an example); constriction of this muscle, which originates from the medial margins of the lower jaw, results in flattening the bottom of the buccopharyngeal cavity and cannot promote a substantial elevation of the copula above its level. Severtsov (1968, p. 161, text-fig. 8) indicated that, in larval caudates, the major role in pressing the tongue to the palate is played by the geniohyoideus muscle. The branchiomandibularis muscle of *Polypterus* and *Amia* provides mostly the ability to masticate and manipulate prey in the mouth (Lauder, 1980b). Thus, the transformation of the coracomandibularis muscle into the geniohyoideus muscle in osteolepiforms was promoted by the increasing contribution of this muscle to the movements of the tongue. It is possible to propose that the initial stage of this transformation was associated with the fact that the coracomandibularis muscle extended when the bottom of the buccopharyngeal cavity was lowered by the sternohyoideus muscle; hence, as the hyobranchial skeleton was retracted, constriction of this muscle directly resulted in rising the copula. The same reasons apparently resulted in the transformation of the coracomandibularis muscle into the branchiomandibularis muscle in ancestors of Actinopterygii. Porolepiform crossopterygians retained a primitive condition of the coracomandibular muscle. This was probably connected with a much lower roof of the oral cavity than in Osteolepiformes; as the palate is positioned low, there is no need for a marked elevation of the copula (and tongue).

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