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The skull and tooth system of *Orlovichthys limnatis*, a Late Devonian dipnoan from Russia

N.I. Krupina, R.R. Reisz, and D. Scott

Abstract: The cranial anatomy of *Orlovichthys limnatis*, a Famennian, Late Devonian dipnoan from the Orel region of central Russia, is described on the basis of an almost completely preserved skull, a mandible, and numerous elements of the dentition. *Orlovichthys* is distinguished from other tooth-plated Devonian dipnoans by its relatively narrow skull and its predatory type of tooth-plate morphology on the pterygoid and prearticular. The marginal dentition of *Orlovichthys*, which extends transversely across the edge of the ossified ethmoid (upper lip) and along the anterior and lateral edges of the dentary, also appears to be organized as tooth plates. The distribution of marginal dentition among Devonian dipnoans and their probable organization as tooth plates prompts us to suggest that an important developmental constraint may have been associated with the dipnoan dentition throughout the long history of this group.

Résumé : L'anatomie crânienne de *Orlovichthys limnatis*, un Dipneuste du Dévonien tardif (Famennien) provenant de la région de l'Orel, en Russie centrale, est décrite en se basant sur un crâne presque complètement préservé, une mandibule et de nombreux éléments de la denture. *Orlovichthys* se distingue des autres Dipneustes dévoniens à complexe palatin par son crâne relativement étroit et la morphologie de son complexe palatin de type prédateur sur la ptérygoïde et le préarticulaire. La denture marginale d'*Orlovichthys*, qui s'étend transversalement à travers le bord de l'ethmoïde ossifié (lèvre supérieure) et le long des bords antérieur et latéraux du dentaire, semble aussi être organisée en complexe palatin. La distribution de la denture marginale chez les Dipneustes du Dévonien et leur organisation probable en complexe palatin nous poussent à suggérer qu'une contrainte importante de développement fût peut-être associée à la denture des Dipneustes tout au cours du long historique de ce groupe.

[Traduit par la Rédaction]

Introduction

The specimens described here come from the Turgenev beds of the Plavsk Horizon (middle Famennian, Late Devonian) exposed in the Rybnitsa locality (Orel region of central Russia). The locality is an exhausted limestone quarry, located on the edge of the Rybnitsa River, approximately 2 km from its confluence with the Oka River. This locality has yielded an unusually diverse assemblage of Famennian ichthyofauna, and is especially rich in lungfish remains (7 genera, 10 species; Krupina 2000).

Orlovichthys limnatis was initially erected on the basis of a mandible and tooth plates (Krupina 1980). Subsequently, the snout (Novitskaya and Krupina 1985) and the skull roof (Krupina 1986) of this form were described briefly. This study provides a detailed cranial description of *O. limnatis*, based on 12 specimens, including: PIN 3725/101, the holotype mandible of a juvenile individual; PIN 3725/102 and PIN 3725/103, prearticular tooth plates; PIN 3725/106 and PIN 3725/107, rostral (ethmoidal) part of juvenile and adult individuals, respectively; PIN 3725/110, the undistorted skull roof and endocranium of a juvenile individual; PIN

3725/116, pterygoid tooth plate; PIN 3725/117, mandible with tooth plate of juvenile individual; PIN 3725/119, isolated prearticular with tooth plate. The specimens were prepared through a combination of mechanical and chemical (10% solution of acetic acid) techniques.

The superb preservation of the dentition has allowed us to present a functional interpretation of the tooth system of *Orlovichthys*. The unusual dental pattern of this dipnoan has led us to conclude that its feeding strategy is significantly different from most of the other tooth-plated Devonian dipnoans.

Rostral region

Three specimens, two juveniles and an adult provide information on the ossified rostral (ethmoidal) region of the skull. The largest specimen, PIN 3725/107, is approximately 3.6 cm at its maximum width and also represents the largest known individual (Fig. 1). This specimen also has the most extensive cosmine cover that includes the two anterior, marginal tooth plates (r.tp), permitting only the ventral exposures of the tips of individual teeth. In strong contrast, the most juvenile specimen that can be attributed to this species on the basis of

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its anatomy (PIN 3725/106), is only 1/3rd the size of the above specimen and exhibits a very thin cosmine layer (Novitskaya and Krupina 1985, pl. VIII, figs. 3, 4). The tooth plates lying on either side of the midline on the ventral surface of the rostral ossification are completely exposed, including the plate proper and the individual teeth that arise from it. In the largest specimen, the ventral surface is occupied posteromedially by large, deep cavities for the nasal capsules. These are separated by a comparatively high, broad internasal septum (s.n, Fig. 1A). The anteromedial part of the ventral surface begins behind the base of rostral tooth plates and continues until the beginning of the internasal septum and is partially separated from the nasal cavities by low cristae. Medially and posteromedially the region of the nasal capsules is overlapped by ventrolateral wings of the "vomeral" (v) area (Jarvik 1980, fig. 307). Anteromedially the nasal cavities pass into the long, broad grooves of the nasal canals. The nasal canals are restricted anteriorly by the subnasal cristae. The lateral border of the nasal cavities is slightly curved, dividing them from the recesses that apparently lodged the lateral nasal veins.

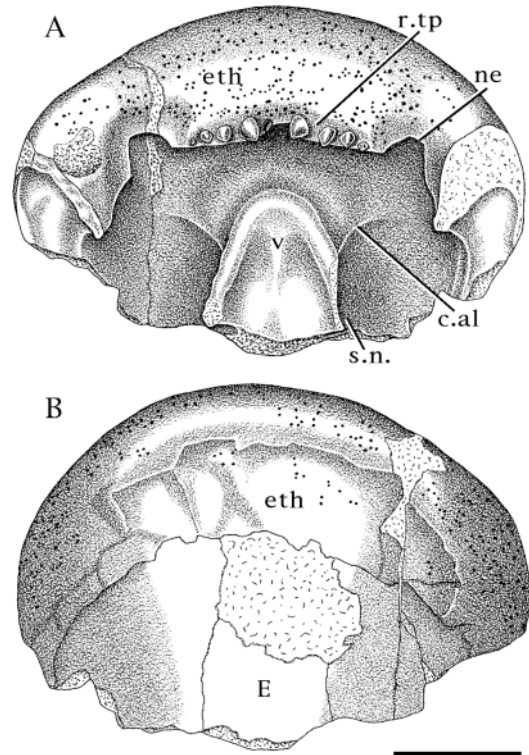
The internasal septum merges with the vomeral area, which is raised highly above the ventral surface of the rostral region. Its anterior border is slightly narrowed and rounded, whereas its lateral walls diverge posterolaterally and slightly downwards, forming wing-like projections that border laterally the nasal cavities.

The posterolateral wing-like projections of the vomeral area and of the internasal septum form dorsolateral grooves of large diameter apparently for the passage of the olfactory nerves (I) that extended to the nasal capsules.

At the anterolateral sections of the floor of the nasal cavities (Figs. 2, 3), just where they pass into grooves for the nasal canals, there are small, rounded openings for one of the branches of the profundus nerve (prof). Smaller foramina of the nasal canal open on the anterior part of the neurocranium dorsolaterally to the openings for the olfactory nerve. Poorly defined grooves in the anterior parts of the orbito-nasal canals (onc), extend from that opening. The grooves pass ventrolaterally along the wing-like projections of the vomeral area.

The planum antorbitale is well ossified. It has the shape of a short, laterally elongated trapezoid at the level of the beginning of the subnasal crista. Obliquely oriented oval foramina of the olfactory canals (I) are the largest openings in this area (Figs. 2B, 3A). They are situated in the midpart of the depressions, lodged in the nasal sacs, at the level of the posterior section of the internasal septum. Adjacent to them are the notches of deep, paired grooves for the lateral branches of the profundus nerve. Mediodorsally to the foramina of the olfactory nerves, there are large rounded openings for the main branches of the ophtalmicus profundus nerve. Lateral sections of the planum antorbitale are pierced by foramina of the supraorbital canals. Exposed on the left side of the dorsal surface of the rostral region, usually covered by the skull roof is the opening for a lateral branch of the v. ophtalmicus superficialis situated between the groove for the lateral branch of the profundus nerve and a groove of the supraorbital canal. Planum antorbitale, in its lateral part, is perforated by paired foramina of the joint orbito-nasal canal. Lateral to the olfactory canal there is a

Fig. 1. Rostral (ethmoid) ossification of *Orlovichthys limnatis* Krupina in ventral (A) and dorsal (B) views, PIN 3725/107. c.al, anterolateral crista of the nasal septum; eth, ethmoid; ne, notch for the external nostril, r.tp., rostral tooth plate; s.n., nasal septum; v, vomeral area; E, E bone. Scale bar = 1 cm.



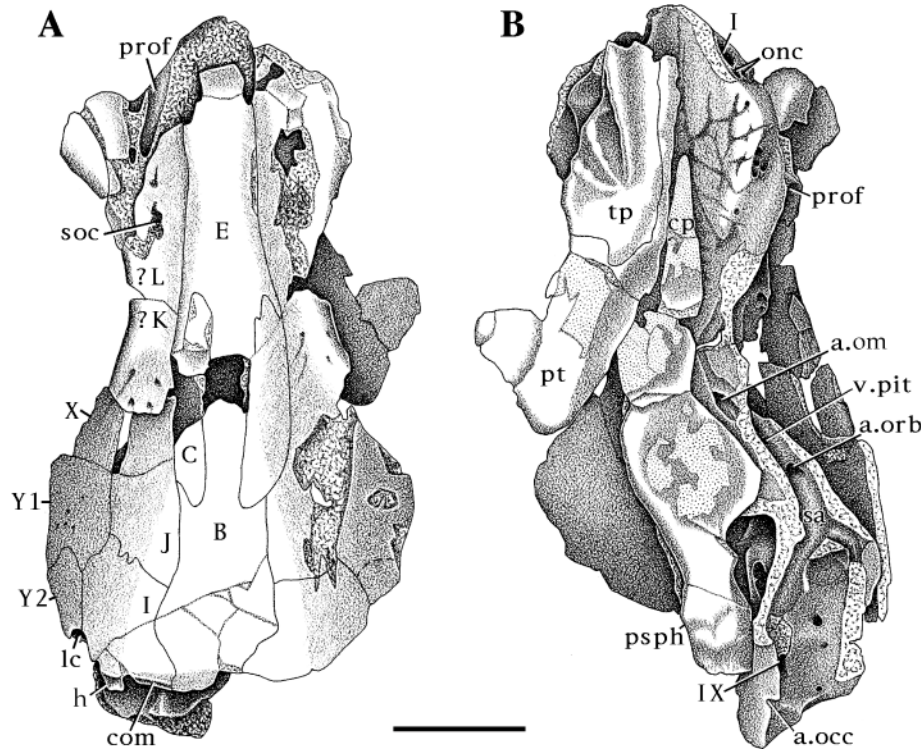
group of small openings for the 1st, 2nd, and 3rd branches of the nervus ophtalmicus profundus.

On the dorsal surface of the rostral region (Fig. 1) the ossified anterior extent of the skull is covered almost entirely by cosmine, and consequently, no distinct ossifications of the rostral (ethmoid) region can be discerned. The skull roofing element identified as the single median E bone extends onto the snout.

Dermal skull roof

In contrast to the excellent preservation of the endocranium, the skull roof is represented by poorly ossified, thin, dermal elements that show little relief and no cosmine cover. This unusual condition is probably a consequence of the immaturity of the specimen PIN 3725/110 (Figs. 2–4). This is also supported by the small size of the pterygoid tooth plate preserved on this specimen (Fig. 2B), and is much smaller than the best preserved isolated tooth plate PIN 3725/116 (Fig. 10). In addition, comparisons between the width of the E bone in the anterior region of PIN 3725/110 (Fig. 2A) and that of the large rostral region of PIN 3725/107 (Fig. 1B) also indicate that the former belongs to a small, juvenile individual. Much of the skull roof is preserved, but numerous cracks and breaks make determination of the suture patterns difficult. Despite this problem, careful examination of the skull roof with frequent use of solvents has allowed us to discover most of the boundaries between

Fig. 2. Skull of *Orlovichthys limnatis* Krupina, PIN 3725/110 in (A) dorsal and (B) ventral views. a.om, foramen for ophthalmic artery; a.occ, foramen for the occipital artery; a.orb, foramen for orbital artery; com, posterior commissure; cp, cultriform process; h, posterior process of skull roof; lc, lateral commissure; onc, openings of the orbito-nasal canal; prof, openings of the profundus nerve and its branches; psph, parasphenoid; pt, pterygoid; sa, groove for lateral dorsal aorta; soc, supraorbital canal; tp, tooth plate; v.pit, foramen for the pituitary vein; capital letters refer to dermal skull bones, roman numerals refer to cranial nerves. Scale bar = 1 cm.



the component bones. It is the unusual pattern of these bones that led us to reconsider briefly this skull roof.

The skull roof is characterized by the presence of relatively few, large, elongate elements, suggestive of extensive fusion (Fig. 2A). The supraorbital region is narrow, giving the skull a slender, elongate appearance. All the elements of the central series are slender and elongate, most notable among these is the unpaired bone tentatively identified here as an E bone. It is not possible to determine if the slender paired C bone reached the midline, because this area of the skull is damaged. Yet, the preserved portions of the slender C bones are widely separated by the median E and B bones. The narrow space between the E and B bones, which is not preserved, could have been occupied by a small D bone, but a more likely scenario is that this space was occupied by the paired C bone. Even if this were the case, the midline suture of the latter would have been quite short. Although the suture pattern is difficult to discern in the posterior region of the skull roof, it appears that the B bone is also an unusually long median element, with its posterior portion being slightly more expanded laterally than its anterior process. The position of the commissure indicates that perhaps an A bone was also present, but this is uncertain.

The passage of the supraorbital canal (soc, Fig. 2A) can be traced by the pattern of small openings that pierce the bones immediately lateral to the C and E bones (Fig. 2A). Similarly, the passage of the cephalic division of the main

lateral line can be traced on the Y bones, immediately lateral to the I and J bones.

The dermal ossifications on the ventral side of the skull in *Orlovichthys* PIN 3725/110 have been preserved only partially (Fig. 2B). The almost complete left pterygoid (pt) bone is poorly preserved, but appears to be relatively thin, narrowly elongated, and positioned along the midline axis of the skull. Its posterior part, free from the pterygoid tooth plate, is approximately equal in length to its anterior half. The parasphenoid (psph, Fig. 2B) is also poorly preserved, but its unusual shape can be discerned. It is greatly elongated anteroposteriorly (total length 36 mm), double-edged with long, narrow, anterior and posterior ends, and broadly expanded in its central part. The ventral surface appears to have been covered by cosmine-like material, which has been preserved as local patches. This is unexpected in view of the fact that the dorsal skull roof elements lack cosmine. In addition, cosmine is normally associated with external surfaces, not areas that would be covered in oral mucosa. The long anterior extension of parasphenoid (cp, Fig. 2B) separates partially the pterygoids, an unusual primitive feature that is only found in some Early Devonian forms like *Uranolophus* (Denison 1968).

The general outlines of the pterygoids, the shape of the parasphenoid and the ventral part of the skull, together with the comparatively narrow angle of divergence of the lower jaw rami (Krupina 1980) and comparatively narrow, elon-

Fig. 3. Skull of *Orlovichthys limnatis* Krupina, PIN 3725/110 in (A) right and (B) left lateral views. a.a.l and a.a.r, left and right anterior ampullary chamber, respectively; a.occ, foramen for the occipital artery; a.orb, foramen for orbital artery; a.p, posterior ampullary chamber, c.l, lateral crista; cp.l and cp.r, left and right posterior canal, respectively; d.sk, dermal skull roof; h, posterior process of skull roof; onc, orbitonasal canal; prof, posterior openings of the profundus nerve and its branches in the ethmoidal region; prof + v.ju, opening for the profundus nerve and internal jugular vein; pt, pterygoid; psph, parasphenoid; ru, recessus utriculi; s, floor for sacculus; so.ca.p, posterior division of the supraotic cavity; ss, sinus superior; tp, tooth plate; v.ca, canal for the v. cerebialis anterior; v.pit, foramen for the pituitary vein; roman numerals refer to cranial nerves. Scale bar = 1 cm.

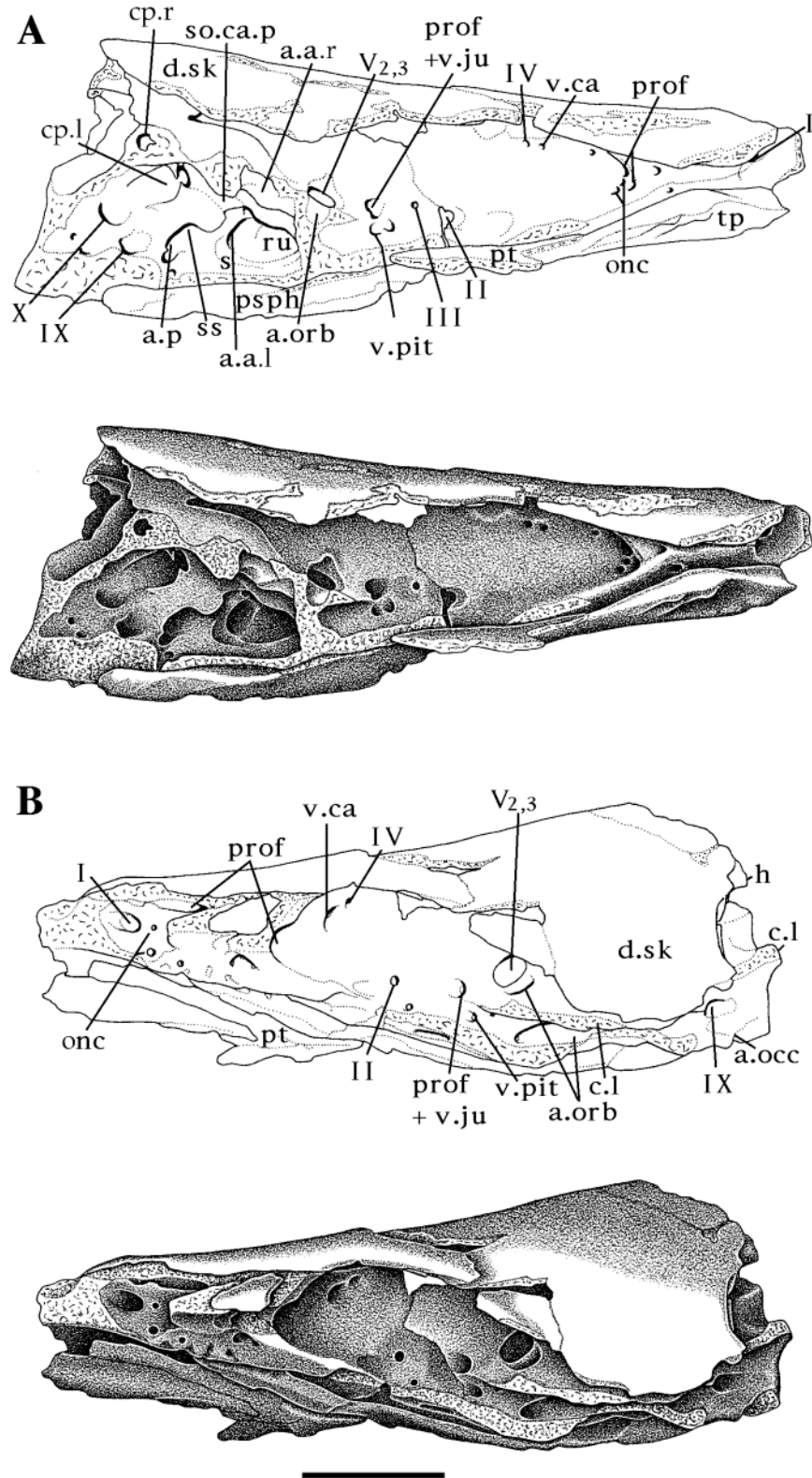
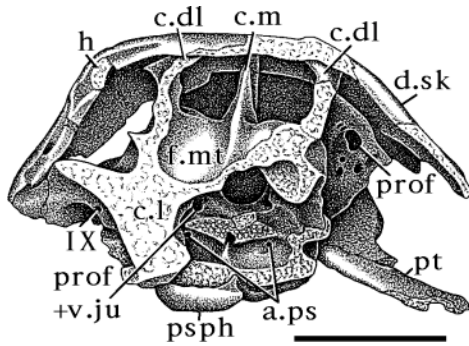


Fig. 4. Skull of *Orlovichthys limnatis* Krupina, PIN 3725/110 in occipital view. a.ps, groove and foramen for the orbital artery; c.dl, dorsolateral crista; c.l, lateral crista; c.m, medial ridge; d.sk, dermal skull roof; f.mt, fossa for the m. temporalis; h, posterior process of skull; prof, openings of the profundus nerve; prof + v.ju, opening for the profundus nerve and internal jugular vein; psph, parasphenoid; pt, pterygoid. Scale bar = 1 cm.



gated anterior bones of the skull roof, indicate that the cranium of *Orlovichthys limnatis* is narrower than most other tooth-plated dipnoans. However, there is no direct evidence for snout elongation of the type seen in some Dipnoi (Miles 1977).

Orbito-temporal region

The ventral and lateral surfaces of the orbito-temporal region of the neurocranium are completely ossified in *Orlovichthys*, whereas the mostly cartilagenous dorsal surface was not preserved (Figs. 2B, 3A, 3B). In keeping with the general proportions of the dermal skull roof of *Orlovichthys*, the orbito-temporal region is much longer than the rostral region, and rather narrow and elongated. The anterior end is appreciably broadened due to the presence of lateroventral projections.

The lateral surface has the outline of a narrow, elongated triangle (Fig. 3). The anterior part, situated behind the planum antorbitale, is pierced by large, obliquely oriented oval foramina of the profundus canal and by openings of the orbito-nasal canal. Farther posteriorly on the lateral surface is the foramen for the anterior cerebral vein, and ventrally to it on the central portion of the lateral surface is the large foramen for nervus ophthalmicus (II). Posterior to the foramen for the anterior cerebral vein and slightly dorsally to it is a comparatively small foramen for the nervus trochlearis (IV). Posterior to the foramen for the ophthalmic nerve and slightly dorsally to it is the small opening for the nervus oculomotorius (III).

The posterior ramus of the palatoquadrate is fused to the neurocranium in the posterolateral section of the orbito-temporal region. This ramus is partly preserved only on the left side of the endocranium (Figs. 2B, 3B). The anterior end of the ascending process of the palatoquadrate is marked by the broad, anteriorly directed foramen for the profundus nerve and internal jugular vein (prof + v.ju, Figs. 3A, 3B). Immediately beneath the ascending process is the large foramen for the pituitary vein (v.pit). The posterior end of ascending process is marked by a very large oval opening for the maxillary and mandibular branches of the trigeminus nerve

($V_{2,3}$). Obviously, this foramen in *Orlovichthys* also carried the facial nerve, as it is shown in the reconstruction of the neurocranium of *Dipnorhynchus sussmilchi* by Campbell and Barwick (1982, fig. 14). Narrowly separating this foramen by a thin lamina of bone is another large, oval opening, presumably for the orbital artery (a.orb). The latter foramen is preserved in its entirety on the left side, but is partially breached by a break on the right side of the neurocranium.

The ventral surface of the orbito-temporal region of *Orlovichthys* is broadened in its anterior part and becomes narrower posteriorly. The medial section of the ventral surface forms a gently sloping, longitudinal groove that extends dorsal to the anterior part of the parasphenoid and continues to the area of medial contact of pterygoids. This groove lodged the paired palatal arteries and nerves. Approximately in the centre of the ventral surface, at the central portion of the orbital depression, is the medially curved groove for the internal carotid artery, which has the same position as in *Chirodipterus wildungensis* (Gross) (Säve-Söderbergh 1952, fig. 1), and the opening of the ophthalmic artery (a.om, Fig. 2B).

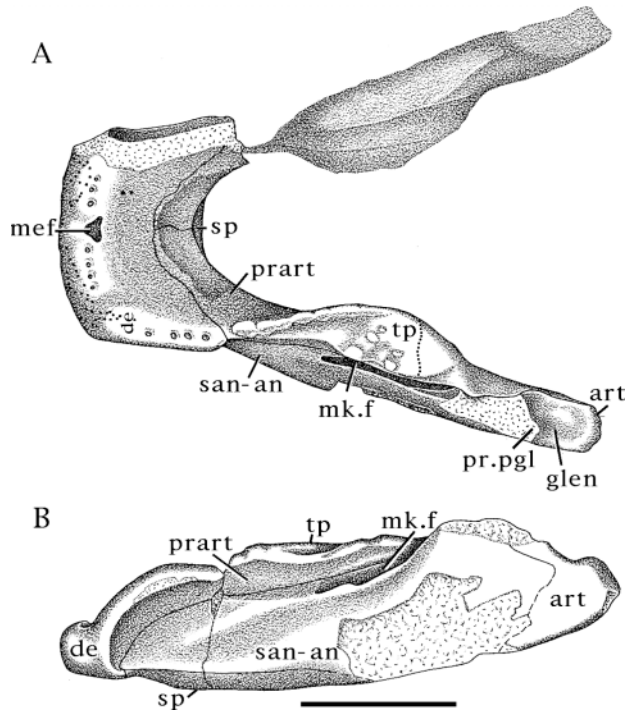
Otico-occipital region

The otico-occipital region of the endocranium begins just posterior to the foramen of the maxillary and mandibular branches of the trigeminus nerve ($V_{2,3}$), and behind the anterior foramen for the orbital artery (a.orb, Fig. 3A). Its anterolateral sections are the continuation of the palatoquadrate bone. The otico-occipital region in its posterior part has three cristae: two paired and one unpaired. One of the paired cristae is comparatively tall and large, and extends dorsolaterally; its posterior part is fused to the skull roof. Occupying a more anterior position is a less steeply sloping paired lateral crista, which is a continuation of the palatoquadrate projection. In its medial part the otico-occipital region is divided by a short, thin unpaired medial ridge.

The labyrinth cavity is located in the space between the skull roof and both paired cristae, and has an oblique oval shape in cross-section. Its size and shape in *Orlovichthys* indicates that the otic part of its otico-occipital region was rather elongated, high, and broad. In general, the length of the otico-occipital region is approximately the same as that of the orbito-temporal, but the former has a maximum width that is about 1.4 times greater.

Preservation of available material provides the opportunity to describe the dorsal, dorsolateral, and ventrolateral surfaces of the otico-occipital region (Figs. 3A, 4). It may be conditionally accepted that the dorsal surface, located between dorsolateral cristae, begins behind the opening for branches of the trigeminus nerve. Farther posteriorly it forms paired posteromedial notches. Dorsally the unpaired median ridge (c.m, Fig. 4) contacts the inner side of the skull roof, and its base divides the posterior part of the dorsal surface of the otic section between the two dorsolateral cristae (c.dl). On the lateral surface of the otico-occipital region, on either side of the large pillar-like median ridge (c.m), is a distinct, well-developed, dorsolaterally facing fossa to which probably attached the dorsal part of m. temporalis (f.mt, Fig. 4). Posterior to the fossa and between both paired cristae the lateral wall of the otico-occipital region forms the bottom of the labyrinth cavity.

Fig. 5. Mandible of *Orlovichthys limnatis* Krupina, in occlusal (A) and left lateral (B) views, PIN 3725/101. art, articular; de, dentary; glen, glenoid area of articulation; mef, median foramen; mk.cav, meckelian cavity; mk.f, meckelian fossa; prart, prearticular; pr.pgl, preglenoid process; san-an, surangular-angular; sp, splenial; tp, tooth plate. Scale bar = 1 cm.



Posterolaterally to the foramen of the orbital artery is a short, rounded process that marks the position of the ampulla of the lateral semicircular canal (a.a, a.p, Fig. 3A). The wall of the neurocranium has been broken away, exposing the internal area where the various semicircular canals and sacs (sinuses) were housed (c.pl, c.pr, ru, s, so.ca.p, Fig. 3A).

The lateral crista (c.l, Fig. 4) begins slightly anterior to the position of the foramen for branches of nerve $V_{2,3}$, and the anterior foramen for the orbital artery. It extends to the end of the occipital part of the region and bears a series of grooves and openings for vessels and nerves. A large foramen for the nervus ophthalmicus profundus, and the internal jugular vein opens anteroventrally to the foramen for branches of nerve V. The groove for the internal jugular vein is broad and deep and runs along the whole ventrolateral surface of the otico-occipital region.

On the lateral side of the otico-occipital region are the well-developed foramina for main blood vessels. A large foramen of the orbital artery is above the groove for the internal jugular vein, whereas below it in an elongated fossa are two foramina, a large foramen of the canal for the pseudobranchial artery and a smaller one for the internal carotid artery. Farther posteriorly is a depression, in which is located a small opening of the glossopharyngeal nerve (IX).

A very large anteromedial foramen for the vagus nerve and the posterior cerebral vein (X) opens in the posteroventral section of the groove for the internal jugular vein. The foramen for the vertical canal of the occipital

artery (a.occ, Figs. 2B, 3B) opens at the ventral surface of the otico-occipital region into the groove for the lateral dorsal aorta (sa, Fig. 2B).

The shallow, broad fossa for the supratemporal branch of the vagus nerve (X), connecting through several narrow openings that pierce the lateral crista, is situated posterodorsally to the foramen for the vagus nerve. In addition, there are a series of small foramina for the spino-occipital nerves, situated posterodorsally and posteroventrally to the foramen for the vagus nerve. The ventral surface of the endocranium has been lost.

The mandible

The most complete mandible is that of an immature individual PIN 3725/101 (Fig. 5), which is slightly smaller than the specimen preserving the skull roof. A much larger fragmentary mandible is represented by PIN 3725/123 (Fig. 6), whereas other mandibular fragments are intermediate in size (Figs. 7–9). The mandible of *Orlovichthys* is relatively short, but narrow. The angle of divergence between the rami is approximately 30° . The symphyseal region is comparatively large, equaling nearly $1/4$ the mandibular length. However, this ratio is probably related to immaturity, and the ratio appears to be smaller in the much larger but incompletely preserved adult specimen (Fig. 6). Posterolateral wings of the dentary extend from the symphyseal region and have relatively broad lateral surfaces, which form up to $1/4$ of the length of mandible.

The maximum number of dermal bones in the mandible of Palaeozoic dipnoans is seven, as found in the Devonian genera: *Dipnorhynchus*, *Chirodipterus*, and *Holodipterus*, and probably represents the primitive dipnoan condition (Miles 1977). The internal series of dermal bones includes the prearticular and a small, single median adsymphyseal plate. The external series includes the dentary and the splenial, postsplenial, angular and surangular. During the evolution of the group, there is a tendency to reduce the external series of dermal bones through fusion. This tendency is well illustrated by *Orlovichthys*, which loses the boundaries between the dentary and adsymphyseal plate, the splenial and postsplenial, and the angular and surangular (san-an, Figs. 5, 6).

The dentary (de) bone in *Orlovichthys* appears to fuse readily with the prearticular (prart), splenial (sp), and postsplenial. The most anterior section has a rounded outline. Ventrally, the dentary is confluent with the adsymphyseal plate and medially with the prearticular. The boundaries between dentary and adjoining bones are difficult to discern because of the overlying cosmine layer. A series of small, low, rounded teeth that pierce the cosmine sheet extend along the edges of the rectangular outline of the dentary. The largest teeth are located anteromedially and on the posterolateral sections of the dentary.

The adsymphyseal plate, which is usually situated directly posterior to the dentary, is only recognizable in *Orlovichthys*, by its topography. The anterior border of adsymphyseal plate in *Orlovichthys* is located near the posterior margin of the triangular foramen (mef, Figs. 5, 6) which is apparently homologous to the deep medial pit or "anterior furrow" in *Holodipterus gogoensis* (Miles 1977, fig. 108a).

Fig. 6. Partial mandible of *Orlovichthys limnatis* Krupina in occlusal view, PIN 3725/123. de, dentary; mef, median foramen; prart, prearticular. Scale bar = 1 cm.

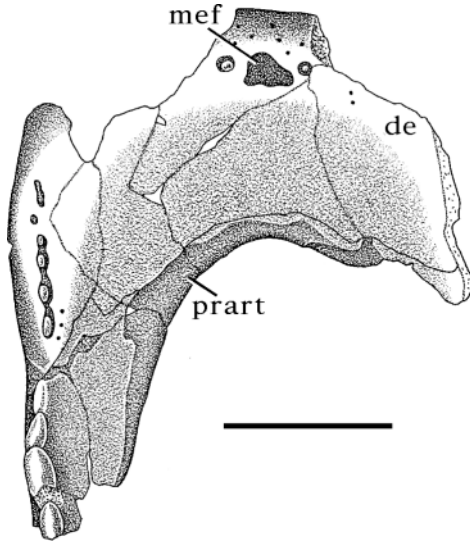


Fig. 7. Dentary of *Orlovichthys limnatis* Krupina in dorsal (A), occlusal (B), and posteroventral (C) views, PIN 3725/115. mef, median foramen. Scale bar = 1 cm.

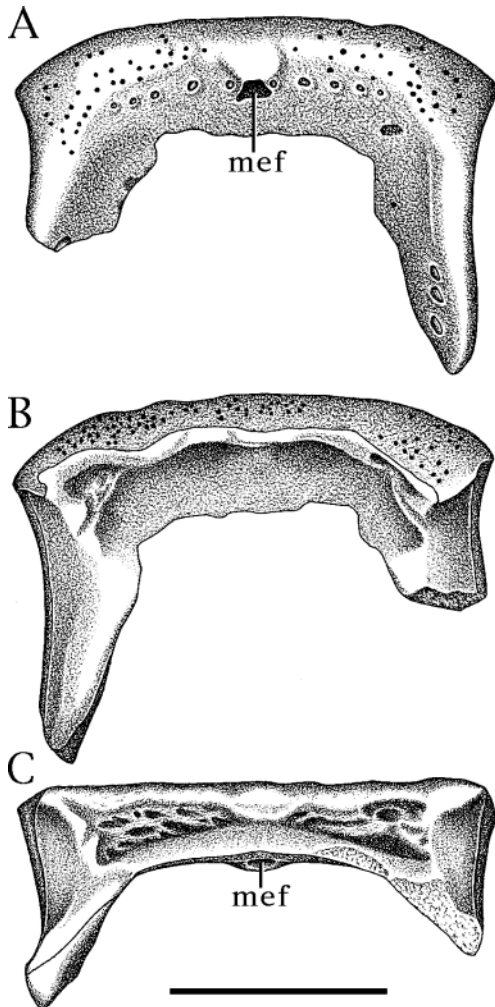


Fig. 8. Partial mandible with prearticular tooth plate, *Orlovichthys limnatis* Krupina in lateral (A), medial (B), and occlusal (C) views, PIN 3725/117. prart, prearticular; tp, tooth plate. Scale bar = 1 cm.

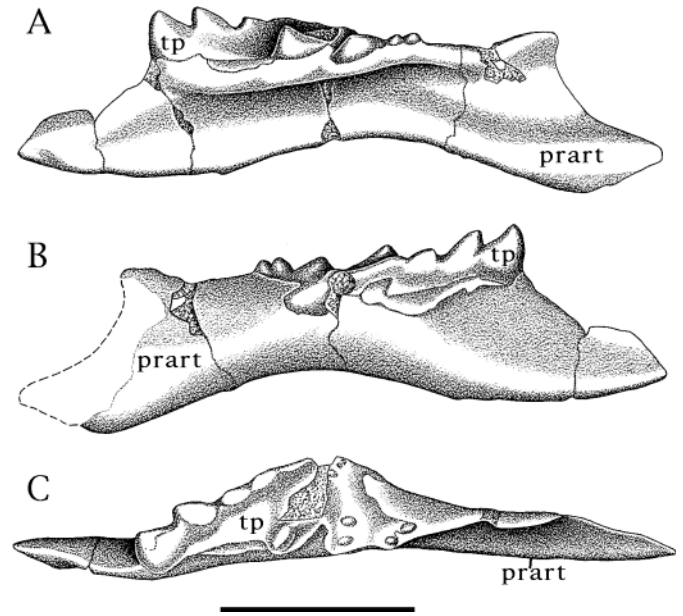
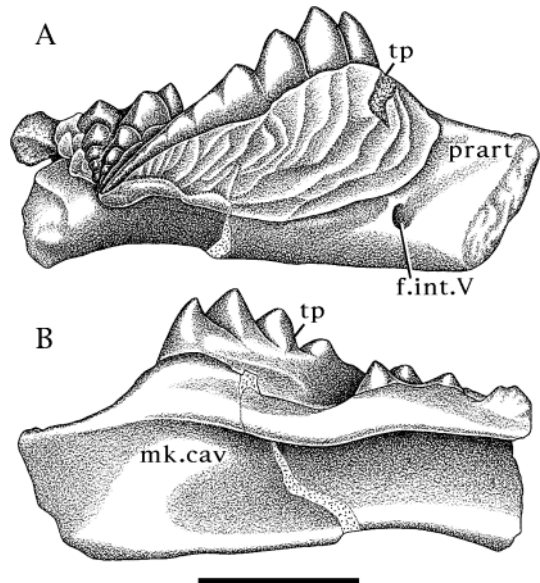
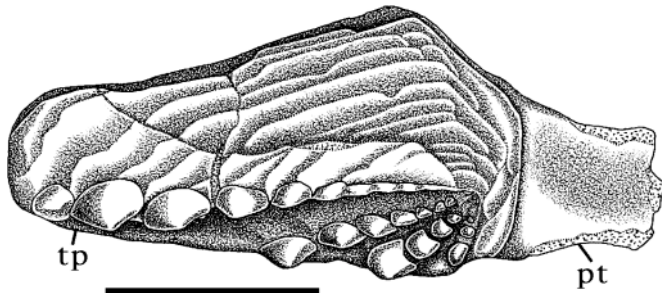


Fig. 9. Prearticular bone with its tooth plate, *Orlovichthys limnatis* Krupina, in medial (A) and lateral (B) views, PIN 3725/129. f.int.V, opening for ramus intermandibularis V; mk.cav, meckelian cavity; prart, prearticular; tp, tooth plate. Scale bar = 1 cm.



The prearticular bone is the largest element of the mandible, is divided on lateral and medial portions, and contacts its sister pair in the symphyseal area just posterior to the dentary. Most Paleozoic and modern lungfishes retain a median prearticular suture. However, some Paleozoic forms, including *Orlovichthys*, lose this suture in the adults (prart, Fig. 6), retaining it only in juvenile individuals (Fig. 5A). The medial portion of the prearticular of *Orlovichthys* resembles that described by Gross (1956, fig. 18) in

Fig. 10. Pterygoid tooth plate of *Orlovichthys limnatis* Krupina, PIN 3725/116. pt, pterygoid; tp, tooth plate. Scale bar = 1 cm.



Rhinodipterus secans, except in being relatively short and lacking a medial depression. The lateral exposure of the prearticular (prart, Fig. 5B) is relatively tall and carries the large tooth plates. Anteriorly the prearticular extends to the symphysis and posteriorly forms the ascending process, overlapping the medial sections of mandibular ramus. The medial surface of the prearticular, beneath the tooth plate appears to be covered by cosmine. In contrast, the external surface, situated below and posterior to the tooth plates, which forms into the broad and low ascending processes, is smooth and appears to represent perichondral bone tissue.

The glenoid fossa (glen) and preglenoid process (pr.pgl, Fig. 5A), which served for attachment of adductor musculature, occupy the main part of articular surface. The articular surface is narrow, elongated, and forms a significant part of the mandible. The glenoid fossa of *Orlovichthys* resembles the fossa in the Late Devonian *Rhinodipterus secans* (Gross 1956, fig. 18). It is comparatively large, deep, and elongated, posteromedial to the rest of the articular are. It differs from that of *Holodipterus* (Miles 1977, figs. 108, 109), which has a posterodorsal, terminal glenoid fossa. The preglenoid process of *Orlovichthys* forms a small low tubercle, located anterolaterally to the glenoid fossa. Based on some specimens of Upper Devonian *Holodipterus gogoensis* and *Griphognathus australis*, this process is incompletely ossified and sometimes is poorly seen in relief (Miles 1977).

The infradental series of bones in dipnoans includes the splenial, postsplenial, angular, and surangular. They are only preserved in the juvenile mandible of *Orlovichthys* (PIN 3725/101). In many lungfishes these bones fuse together and their sutures are lost, and boundaries can be established only tentatively on the basis of sensory canals. The angular in *Orlovichthys* fuses with the surangular into a single bone on the lateral surface of the mandible (san-an, Fig. 5). The lateral outline of the surangular-angular has the shape of an acute triangle with an anterior angle of approximately 25°. Its lateral surface lacks a cosmine cover. In spite of the absence of a clear suture between the angular and surangular, a vague boundary between them is visible in relief. The otic and mandibular sensory canals run along the lateral side of the bone, and join at the level of the first tooth ridge of the prearticular tooth plate. They can not be seen along their entire length, the mandibular sensory canal being better marked on the ventral side of the dentary, where it opens to the outside through large pores arranged symmetrically in a transverse line across the width of the bone. A distinct splenial ossification can be seen in the juvenile mandible,

this area not being preserved in any other specimen. Interestingly, the juvenile specimen shows a median contribution to the symphyseal region directly beneath the paired prearticulars. There does not seem to be a suture on the left and right sides of the splenial.

Upper jaw dentition

The main tooth elements of the upper jaw in *Orlovichthys*, as in all other tooth-plated dipnoans, are the pterygoid tooth plates (Figs. 2B, 10), located on the anterolateral sections of the pterygoid bones. The plates are elongated and approximately triangular in outline, with a length that is 2–2.5 times the width. Each plate has either three or four ridges that radiate anteriorly and anterolaterally from an apex and bear flattened, large, and sharp teeth.

The overall morphology of the tooth plate is best preserved in the largest known specimen, PIN 3725/116 (Fig. 10). The first, median ridge is most completely developed, much longer than the others, and bears the biggest teeth. Usually, it is difficult to determine the precise number of teeth on each ridge because the oldest (located near the apex) teeth have fused together, forming a continuous sharp surface, whereas the five or six youngest teeth look completely developed and separated. The largest teeth are located near the labial edge of the ridge. The second ridge is lateral to the first and is considerably shorter than the first. The last three teeth are the largest and are well separated from each other. The third ridge is approximately 1/3 the length of the first and bears only three separate teeth. The fourth ridge is poorly developed, only 1/5 of the length of the first, and characterized by the presence of only two separate teeth which are considerably smaller in size than those on the other ridges. Medial to the first ridge is a large, well-developed roughly triangular area of the plate, which is covered by numerous layers of stratified enamel sheets. Its length is subequal to that of the plate.

The anterior region of the upper jaw in the largest specimen of *Orlovichthys* (Fig. 1) is completely covered by cosmine, and has eight exposed teeth on its anteroventral edge. These teeth can be interpreted as exposed portions of the paired rostral tooth plates. They are transversely aligned on the ventral side of the rostral ossification (premaxillae) between the notches of the external nostrils. The plates are completely exposed only in the most juvenile known individual, PIN 3725/106, and are separated by a narrow notch. The plates each bear four sharp conical teeth, in PIN 3725/107, and three teeth in the juvenile PIN 3725/106. The teeth gradually decrease in size laterally and are directed obliquely toward the buccal cavity. Their structure and disposition indicates that they are homologous to the teeth of the rostral plates seen in hatchlings of *Andrejevichthys epitomus* (Krupina and Reisz 1999), whereas the notch between the plates probably represents an area for future growth and development of new teeth.

The presumed third element of the upper jaw dentition were vomerine tooth plates, as indicated by anatomy of the vomeral area of the skull, but no such tooth plates have been recovered from the Rybnitsa locality.

Lower jaw dentition

The main lower jaw tooth elements of *Orlovichthys*, as in all other tooth-plated dipnoans, are paired prearticular tooth plates (Figs. 5, 8–9). These were located on the anterodorsal parts of the mandibular rami and extend parallel to the long axis of skull (Fig. 5). The known examples range from small juveniles, as seen on the mandible of PIN 3725/101, to the adult size represented in PIN 3725/129 (Fig. 9). Despite the great range in size, they all have the shape of an obtuse-angled triangle. The length of the prearticular tooth plate is three times its width. The tooth plates listed above have three unequally developed ridges, diverging from a single point at its apex and bearing high, big, dagger-like teeth, the biggest and the sharpest of which are located on labial portion of each ridge. A third specimen, PIN 3725/117 (Fig. 8C), appears to have two small teeth that may have formed a fourth row. All the plates are arranged along the mandibular rami in such a way that the teeth of the first, greatly elongated ridge forms a row that is continuous with the marginal teeth on the dentary (Fig. 6).

The first ridge is the longest and best-developed of the series. It is slightly curved, bears three to four strong, big, laterally flattened, dagger-like teeth. The largest, sharpest teeth are placed anteriorly on the ridge. Additional (up to a maximum of seven or six) smaller, less distinct teeth extend along the rest of the ridge and fuse into a continuous sharp surface toward the apex of the plate.

The second ridge is significantly shorter than the first, approximately 45% of the length of the latter, and has a maximum of five or six teeth. Distally it also bears separate, sharp teeth, but of smaller size than those on the first ridge. The third ridge is the shortest, being only 35% of the length of the first ridge, is less well developed in the juveniles, and consists of up to 4 separate teeth (PIN 3725/117). As is the case with the pterygoid tooth plate, a large, well-developed area of the plate is present medial to the first ridge, which is covered by numerous layers of stratified enamel sheets. The length of this area is equal in general length to that of the ridged portion of the plate.

In addition to the teeth on prearticular plates, *Orlovichthys* also has teeth along the lateral and anterior rami of the dentary (PIN 3725/101, 115 and 123). These teeth are arranged in single rows, are oriented at approximately 95° to one another, and are partly covered by cosmine. On the lateral ramus of the dentary, the teeth appear to be smaller than those on the first ridge of prearticular plate. This is probably because the dentary teeth are almost completely covered by cosmine, and their reconstructed actual size is similar to those on the tooth plates. These dentary teeth are probably derived from hatchling and juvenile marginal dentition (Krupina and Reisz 1999) and preserve the same ratio in size and disposition as teeth on tooth plates of hatchlings of *Andreyevichthys*. As on those tooth plates, larger teeth are located on the distal portion of the plate, at the posterolateral corner of the dentary, while the smaller teeth are located at the “apex” of the plate, i.e., in the central part that is situated in the bend of the dentary.

A partial mandible of a large, adult individual (PIN 3725/123) lacks the anterolateral corners of the dentary (Fig. 6). Consequently, the plate portion of the tooth system

that is normally covered by cosmine in other specimens is visible in section. The body of the tooth plate is readily distinguishable from the overlying cosmine, because it is black in color, the same as the teeth that pierce the light brown cosmine. Both components of the tooth plate are not only exposed in section, but are also visible slightly around the base of each tooth, where cosmine has failed to attach completely to the sides of the teeth.

In the central part of the dentary of *Orlovichthys*, between the two rows of anterior teeth, there is a deep, large, roughly triangular opening (Figs. 5–7). Its border is slightly raised, forming a small prominence. Careful preparation of this opening has revealed that it is connected to the sensory canals located in the body of the dentary, suggesting a similar function. On either side of this opening is a row of teeth, best preserved in PIN 3725/115 (Fig. 7), that increase in size medially, except for the medialmost tooth, which appears quite small and is located right next to the opening. It is quite obvious that these teeth are also partially buried by cosmine and that the medial teeth that are next to the opening, although probably large, were almost completely buried by the ridge of cosmine that forms the border of the opening.

Discussion

Among known tooth-plated dipnoans, *Orlovichthys* appears to have one of the most elaborate tooth systems. These include not only the pterygoid and prearticular plates, but also tooth plates in the rostral or “preoral” (Miles 1977, pp. 14, 179) region, probably in the “vomeral area” (Jarvik 1980, fig. 307), as well as so-called “labial teeth” (Kemp 1977; Smith and Chang 1990, p. 428) on the dentary. Since all these types of teeth were present in the adult form, it is possible and appropriate to consider the manner in which the opposing tooth elements occluded when the jaws closed in *Orlovichthys*. It is already well known that the pterygoid and prearticular plates occluded in tooth-plated dipnoans (Kemp 1977; Campbell and Barwick 1983; Smith and Campbell 1987). Similarly, the tooth plates of *Orlovichthys* had partial occlusion when the mouth closed, as indicated by wear. More interestingly, it is likely that during closure, the dentary contacted the marginal teeth on the upper jaw, while the sensory opening of the dentary fitted into the gap between the rostral tooth plates. This interpretation is confirmed by traces of shallow furrows on the outer border of the dentary of *Orlovichthys limnatis* (PIN 3725/101 and PIN 3725/115). The furrows were apparently caused by teeth of the rostral plates during occlusion, suggesting that the main body of the dentary fitted into the gap between the edge of the upper jaw and the hypothesized vomerine tooth plate.

The adult dentition of *Orlovichthys* appears to be directly comparable to the relatively early ontogenetic stage (hatchlings) of the tooth-plated Devonian dipnoan *Andreyevichthys* (Krupina and Reisz 1999). The row of teeth on the dentary in *Orlovichthys* also resembles that of *Holodipterus gogoensis* (Smith and Chang 1990). In their initial description of the tooth system of the Early Devonian *Diabolepis speratus* Smith and Chang (1990) compared its dentary dentition to the labial tooth plates of *Neoceratodus forsteri* (Kemp 1977) at an early (ontogenetic) stage of tooth formation. Study of the juvenile dentition of the Late Devonian

dipnoan *Andreyevichthys epitomus* confirms the presence of tooth plates arranged along the lateral and medial sections of the dentary, which are directly comparable to early stages of tooth formation in *Neoceratodus*. Remarkably, *Orlovichthys* appears to have retained these tooth plates in the adult state, although only the tips of the individual teeth are able to break through the cosmine cover of the dentary.

It is noteworthy that the presence of marginal teeth on upper and lower jaw bones is rather common among Devonian dipnoans. Different types of teeth or tooth-like structures on the dentary and the upper jaw margin are present in tooth-plated dipnoans (*Chirodipterus*, *Scaumenacia*), in denticulated forms (*Griphognathus*), and in dipnoans with so-called "Mixed" type of dentition (*Diabolepis*, *Ganorhynchus*, *Holodipterus*, "*Dipterus*" *oervigi*; Miles 1977; Rosen et al. 1981; Smith and Chang 1990; Song and Chang 1991). Notable among these is *Dipterus oervigi* (Gross 1964, fig.3B), which has single-rowed marginal dentitions on the upper jaw margin, consisting of five teeth on either side of the median notch, with the largest in each row being placed medially and on anterior and lateral edges of the dentary. Only few of the anterior, transversely arranged dentary teeth are exposed in the holotype and only known specimen, and six teeth are preserved on the left lateral edge. Direct examination of this specimen reveals that the laterally arranged teeth increase in size posteriorly, but no equivalent pattern can be discerned for the anterior row because too few teeth are exposed. All of these teeth have suffered some preservational damage, the columnar petrodentine being exposed in both the marginal series, as well as in the underlying tooth plates. In the denticulated form *Griphognathus* (Campbell and Barwick 1983, figs. 2 and 4C), there are three or four well-developed teeth on either side of the median notch of the hard upper lip. Some specimens of *Holodipterus gogoensis* (Campbell and Smith 1987, fig. 3A) have marginal teeth developed on both the anterior and lateral margins of the dentary. *Chirodipterus liangchengi* (Song and Chang 1991, fig. 5) also appears to possess three teeth on either side of the median notch of the hard upper lip, whereas *Ganorhynchus woodwardi* appears to have both anterior and possibly lateral marginal teeth on the hard upper lip (Miles 1977 p. 179; Rosen et al. 1981, fig. 8).

The structure of the marginal dentition in the rostral region of *Orlovichthys limnatis* is similar to that in *Ganorhynchus woodwardi* (Rosen et al. 1981, fig. 8), which also has paired tooth plates bearing sharp conical teeth obliquely directed into the buccal cavity. The only significant difference between these structures is the number of teeth present (*Ganorhynchus* has six teeth instead of three to four on each plate).

Between the rostral plates of *Ganorhynchus*, as in *Orlovichthys*, there is a median notch that turns into a deep conical pit. The vomeral area of *Ganorhynchus* is also very similar to that of *Orlovichthys*, suggesting that it also carried vomerine tooth plates during life. Unfortunately, the lower jaw of *Ganorhynchus woodwardi* is unknown, but judging by the structure and disposition of teeth on its rostral region, it is reasonable to assume that, as in *Orlovichthys*, it may have also retained a marginal dentition.

The nature and arrangement of the teeth in the above dipnoans are surprisingly similar to the marginal dentitions

of *Orlovichthys*, providing strong support to the hypothesis that they are also part of tooth plates. Most striking among these similarities is the readily recognizable arrangement of smaller to larger teeth on the snout and the presence of the median notch in the rostral region.

Conclusions

(1) The presence of the well-developed tooth system in *Orlovichthys limnatis* provided effective food processing during jaw closing. The shape and configuration of the teeth of *Orlovichthys* indicates a predatory type of feeding behaviour. The main lower and upper tooth plates were different from those of other Devonian tooth-plated dipnoans in the presence of few ridges, of which the first is the most extensively developed. The largest ridges were arranged not opposite to or at an angle to the long axis of skull, but rather were in line with the long axis of the skull, creating an effect similar to the marginal tooth row of other bony fishes.

The tooth system of the adult *Orlovichthys* is surprisingly similar to the tooth-system construction of hatchlings of the tooth-plated Devonian dipnoan *Andreyevichthys* (Krupina 1992, Krupina and Reisz 1999). The hatchlings of the latter are interpreted as having a predatory mode of life, possessing an unusual type of bite that emphasizes grasping and holding of prey, and a unique way of processing the food.

Our conclusion that the additional tooth elements seen in the adult *Orlovichthys* may be related to a distinct mode of grasping and biting of the prey, are confirmed by data observed by Kemp in hatchlings of modern *Neoceratodus forsteri* (A. Kemp, personal communication, 1996).

It appears, therefore, that in adult specimens of *Orlovichthys limnatis* a tooth-system construction is preserved, which is otherwise seen in the early (hatchling) ontogenetic stages of both living and Devonian dipnoans. This can be explained as an adaptation to a predatory behaviour in the adults. We speculate that the pterygoid and prearticular plates with sharp, dagger-like teeth, with its best developed, longitudinally oriented first ridges, did not grind or crush food like in other tooth-plated dipnoans, but sheared its food item (probably prey). At the same time the food item was probably held in the mouth with the help of the small marginal dentition.

(2) The tooth-system construction of paired pterygoid and prearticular tooth plates with a unique method of adding new teeth labially while retaining all older teeth, appears to provide the greatest advantage in the evolutionary history of dipnoans. This follows not only from the fact that most of the known marine, brackish-water and fresh-water forms possessed just this type of tooth system, but is also supported by the documented diversity and variations in such type of tooth-system construction and modes of functioning of the opposing tooth plates (grinding, grating, crushing, cutting, tearing). All living dipnoans, despite long evolutionary history, have retained this type of tooth-system construction.

The superb preservation of the marginal dentition of *Orlovichthys* allows us to identify them as part of tooth plates that have been subsequently covered over by cosmine. The overall similarity between the marginal dentition of

Orlovichthys and other Devonian dipnoans, such as *Dipterus oervigi*, *Chirodipterus*, indicates that the marginal dentitions of other dipnoans are probably also organized as tooth plates. This possibility emphasizes the need for careful study of marginal teeth in dipnoans through the use of thin sections to identify correctly the nature and provenance of these teeth. However, if this interpretation is correct, then we may be seeing evidence of a fascinating evolutionary and developmental constraint among dipnoans: Once tooth plates have evolved among dipnoans, with their unique method of retaining all the old teeth and adding labially and distally (rather than lingually) new teeth to the plates, the only mechanism for evolutionary change of the teeth appears to be solely in the context of tooth plates. This constraint appears to be best demonstrated by the manner in which some dipnoans (listed earlier in the text) have developed marginal dentition that ancestrally may not have been part of a tooth plate system. This hypothesis does not address the controversy associated with the question of homology of teeth of dipnoans and other sarcopterygians, but does suggest that the tooth-plated condition may represent the primitive condition for dipnoans. Once this unique dipnoan structure was incorporated into the developmental pattern of members of this group, major changes to this system may have been difficult. For example, both fossil *Andrejevichthys* (Krupina and Reisz 1999) and extant (*Neoceratodus* Kemp 1996) marginal dentition could exist only in the context of a tooth plate. Tooth plates that carried either single or multiple rows of teeth, formed the equivalent of the marginal dentition of other bony vertebrates, served to capture prey in the early juvenile stages of these animals, and were subsequently resorbed.

This proposed developmental constraint has major implications to the phylogenetic position of the so-called denticulated dipnoans. These forms may not be basal dipnoans despite the early appearance of such forms as *Uralonophus*, but rather derived taxa, in which the only way to get rid of the tooth plates was to completely eliminate the whole structure, including the teeth. An interesting test of this hypothesis would be to try to find hatchlings or very small juveniles of denticulated dipnoans to examine them for marginal dentition.

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