

# A New Species of *Laccognathus* (Porolepiform Crossopterygii) from the Devonian of Latvia

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**Abstract**—A new species of the genus *Laccognathus*, *L. grossi* sp. nov., from the upper strata of the Gauja Formation of the Main Devonian Field (Lode locality, Latvia) is established. Morphological similarity and differences of the new species from the previously described *L. panderi* Gross from the lower strata of the Gauja and the Amata Formation of Latvia are discussed.

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**Key words:** Porolepiformes, Crossopterygia, Devonian, Latvia.

## INTRODUCTION

The genus *Laccognathus* represented by the only species *L. panderi* was established by Gross (1941) based on the lower jaw fragments, which he collected in the Devonian of the Ermani locality, Latvia. Some cranial and postcranial bones that were initially described as *Dendrodus biporcatus* (Gross, 1930, 1933, 1936) from the same and other localities of Latvia, which were dated by Gross to the Middle Devonian *Asterolepis ornata* and *A. radiata* zones), were also referred to this species (Gross, 1942). Subsequently, these specimens were dated Abavskaya Subformation of the Burtniekskaya Formation and the lower strata of the Gauja Formation of the Main Devonian Field, i.e., the Givetian Stage of the Middle Devonian (Ahlberg, 1998). Vorobyeva et al. (1997) described scales of *Laccognathus* sp. from the Mikhailovskii Mine of the Kursk Magnetic Anomaly of the Central Devonian Field, from the deposits of the Timan Horizon (Frasnian) of the Upper Devonian. This genus was recently recorded in the Upper Devonian (Frasnian) of Canada (Daeschler et al., 2003).

In 1971, an expedition of the Paleontological Institute of the Russian Academy of Sciences headed by the author of the present paper collected unique material of extinct fishes (*Asterolepis ornata*, *Panderichthys*, and *Laccognathus*) in the Lode quarry (vicinity of the town of Cesys, Latvia). These beds were assigned to the terminal Gauja Formation (Frasnian) of the Upper Devonian (Vorobyeva, 1980) or the upper strata of the Gauja Subhorizon (Lyarskaya, 1981). The position of the Givetian–Frasnian boundary in the Baltic Region is recently widely discussed (Forey et al., 2000). This boundary is placed at the level of either the upper strata of the Gauja Formation (Mark-Kurik et al., 1999) or the beds overlying the Amata Formation. In either case, the

Gauja and Lode formations are tentatively referred to the Givetian, i.e., to the Middle Devonian. However, this question remains open.

The *Laccognathus* specimens collected in Lode include several almost complete fishes and skulls; this allowed a detailed study of many morphological features of porolepiform crossopterygians, including some previously unknown characters.

I studied the original material housed in the Paleontological Museum of Berlin (Museum für Naturkunde) and compared the specimens of *L. panderi* collected by Gross with *Laccognathus* from Lode. This comparison has led to the conclusion that the latter should be assigned to a new species (Vorobyeva, 2003), which is described below under the name *L. grossi* sp. nov. In addition, the diagnosis of the genus *Laccognathus* is amended.

## SYSTEMATIC PALEONTOLOGY

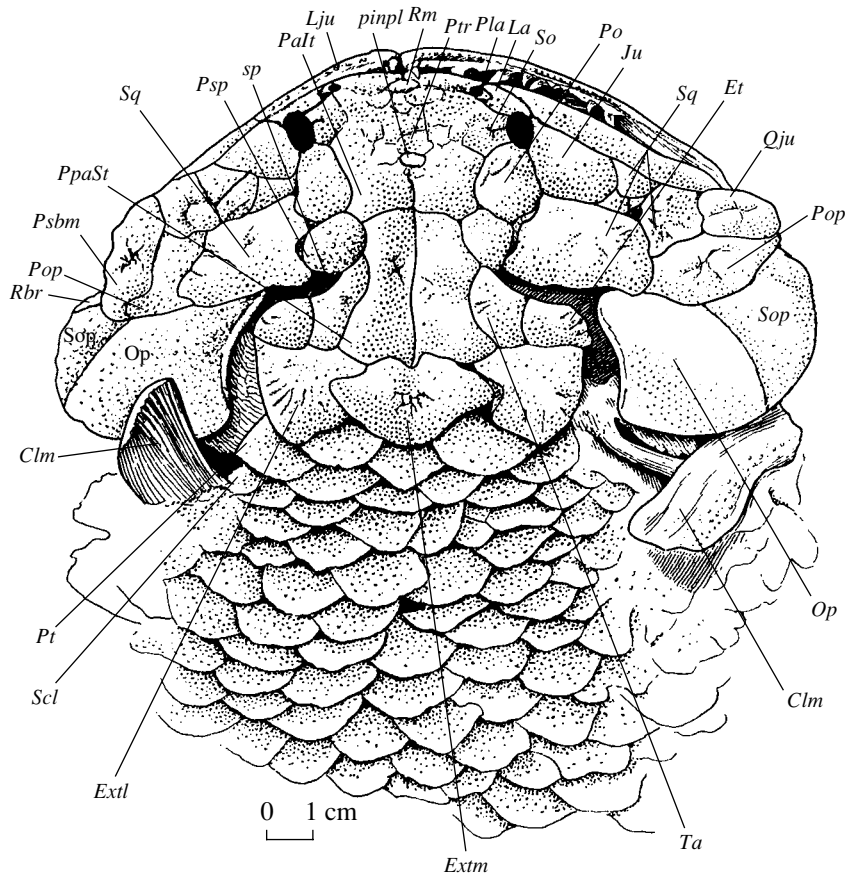
### Family Holoptychiidae Owen, 1860

#### Genus *Laccognathus* Gross, 1941

*Laccognathus*: Gross, 1941, p. 19.

**Type species.** *Laccognathus panderi* Gross, 1941; Middle Devonian of Latvia.

**Diagnosis.** Large fishes, 1–2 m long; body terete. Paired fins with moderately developed fleshy lobes. Head short (less than one-fifth as long as body); snout wide, rounded; skull dorsoventrally flattened. Large single external naris bordered posteriorly by wedge-shaped bone (praelacrimale), which homologous to nariodole of other holoptychiids and rostrale laterale of osteolepiforms (Vorobyeva, 1980, 2004). External incisure of exochoana probably present. Lower jaw short, wide, with three large incisures on external surface and three coronoids, poorly developed anterior infradental



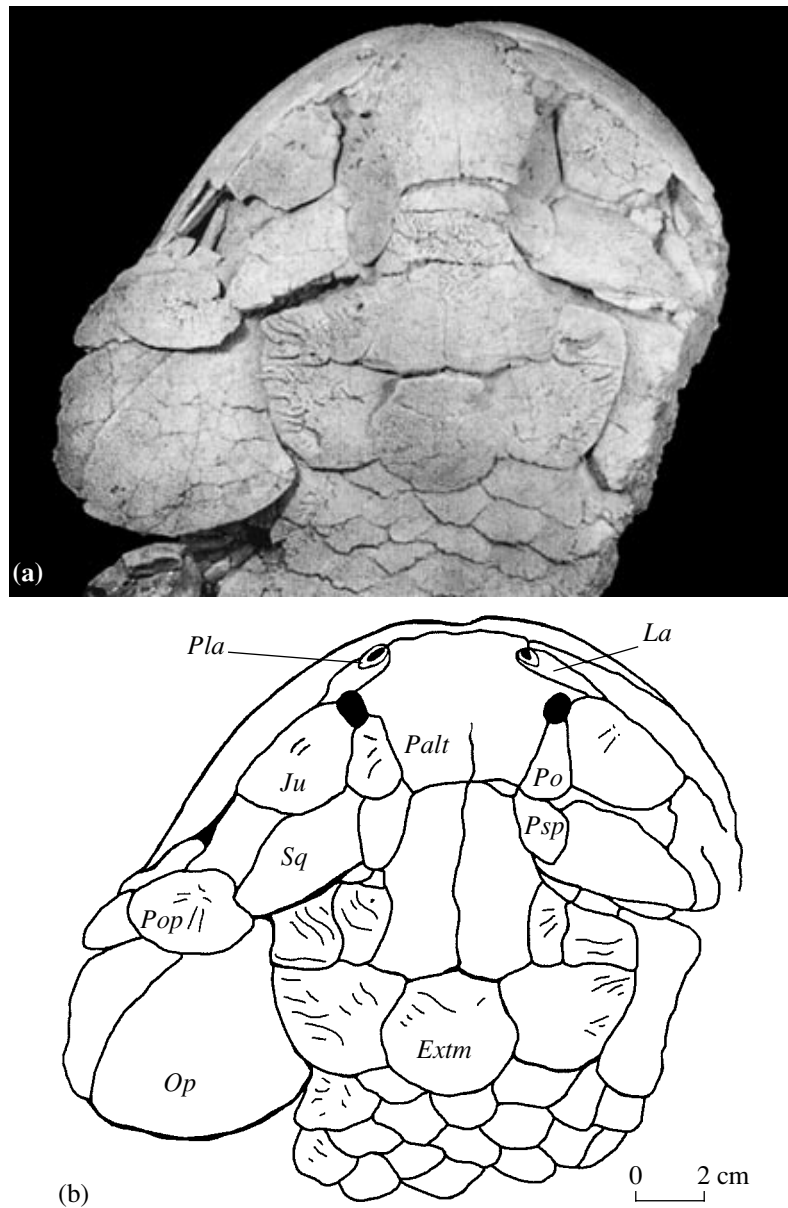
**Fig. 1.** *Laccognathus grossi* sp. nov., reconstruction of the skull roof based on specimen PIN, no. 3547/6. Designations: (*Clm*) cleithrum, (*Et*) extratemporal, (*Extl*, *Extm*) lateral and medial extrascapularia, (*Ju*) jugale, (*La*) lacrimale, (*Lju*) lower jaw, (*Op*) operculum, (*Palt*) parietointertemporal, (*pinpl*) pineal plate, (*Pla*) praelacrimal, (*Po*) postorbitale, (*Pop*) preoperculum, (*PpaSt*) postparietosupratemporal, (*Psbm*) praeoperculo-submandibulare, (*Psp*) praespiraculare, (*Pt*) posttemporal, (*Ptr*) postrostrale, (*Qju*) quadratojugale, (*Rbr*) radii branchiostegi, (*Rm*) rostrale mediale, (*Scl*) supracleithrum, (*So*) supraorbitale, (*Sop*) suboperculum, (*Sq*) squamosum, (*sp*) spiracle, and (*Ta*) tabulare.

flange, and highly positioned mandibular sensory canal. Presymphysial plate positioned transversely, with two or three canines bordered anteriorly and posteriorly by rows of small denticles. Five hyobranchial arches present, anterior three articulated with basibranchiale. Gulare mediale absent. Six submandibularia and five radiobranchialia present. Interclavicula short and wide. Claviculae positioned close to ascending process, which overlapped by cleithrum. Cheek plate with large upper squamosal and several small lower squamosals. Praespiraculare lacking branch of supraorbital sensory canal. Scales, membrane skull bones, and pectoral girdle with denticles. Dental microstructure of dendrodont type.

**Species composition.** Three or four species: *L. panderi* Gross, lower part of the Gauja Subhorizon of the Frasnian and the Burtniekskii Horizon of the Givetian of Latvia; *L. grossi* sp. nov., upper part of the Gauja Subhorizon of Latvia; *Laccognathus* sp., Timan Horizon of the Central Devonian Field; and *Laccognathus* sp., Early–Middle Frasnian of Canada.

**Comparison.** *Laccognathus* differs from other genera of the family in the presence of one external narial incisure and praelacrimal, which borders it posteriorly; in the presence of three large external fossae (incisures) in the lower jaw; in the ornamentation of scales and membrane bones; the absence of gulare mediale; the number and articulation pattern of the hyobranchial arches, the morphology of the praespiracular plate, the shape of the interclavicle, the weakly developed anterior infradental flange; and in the ornamentation of membrane bones and scales.

**Remarks.** In the theses presented at the International Paleoichthyological Symposium devoted to the 100th birthday of Gross, new well-preserved specimens of *Laccognathus* from the Upper Devonian of Canada (Early–Middle Frasnian) were mentioned (Daeschler et al., 2003). These theses provide only little information on this taxon, including the presence of three large incisures on the external surface of the lower jaw, the presence of a prelacrima, single external naris, and the proportions of the roof shields (the parietal shield is slightly shorter than the postparietal shield). The first



**Fig. 2.** *Laccognathus grossi* sp. nov., holotype PIN, no. 3547/7, skull, dorsal view: (a) general appearance and (b) drawing. For designations, see Fig. 1.

two are probably generic characters. The last character is unknown in *L. panderi*. The composition of the accompanying ichthyofauna only partially coincides with that of the localities yielding *L. grossi* and *L. panderi*. The taxonomic status of the Canadian *Laccognathus* remains an open question.

*Laccognathus grossi* Vorobyeva, sp. nov.

*Laccognathus panderi*: Vorobyeva, 1980, p. 195, text-figs. 3B, 4–6; 1992, p. 113, text-fig. 28E; 2004, p. 353, text-figs. 47 and 48, pl. VII, fig. 1; Lyarskaya, 1981, p. 26.

**Etymology.** The species is named in honor of the Professor W. Gross.

**Holotype.** PIN, no. 3547/7, skull; northeastern Latvia, vicinity of Cesys, Lode quarry; Middle Devonian, Givetian Stage, upper part of the Gauja Horizon, Lode Member.

**Description.** The skull roof (Figs. 1–8) is formed by the movably articulated anterior and posterior shields, as in the majority of rhipidistians; the contact line between the shields has a convex apex. The posterior shield is 1.15–1.25 times as long as the anterior shield. In the region of preorbital corners, the width of the shield is greater than its length. The anterior edge of the snout is low, formed by short and relatively high rostro-praemaxillaria. The rostrale mediale (Fig. 1, *Rm*) is located between the upper areas of these bones. The

postrostral series (*Ptr*) is long, reaches the line of the midlength of the anterior shield and wedges deep in between the parietointertemporalia (*Pal*), which form the anterior shield. This series is bordered posteriorly by the pineal plate (*pinpl*), which is usually in the shape of a small expansion on the surface of this shield. This plate reaches caudally the level of the parietal pitted line. The parietointertemporale is more than three times as long as the posterior shield. The width of this bone at the posterior margin is 1.5 times greater than its length along the medial suture.

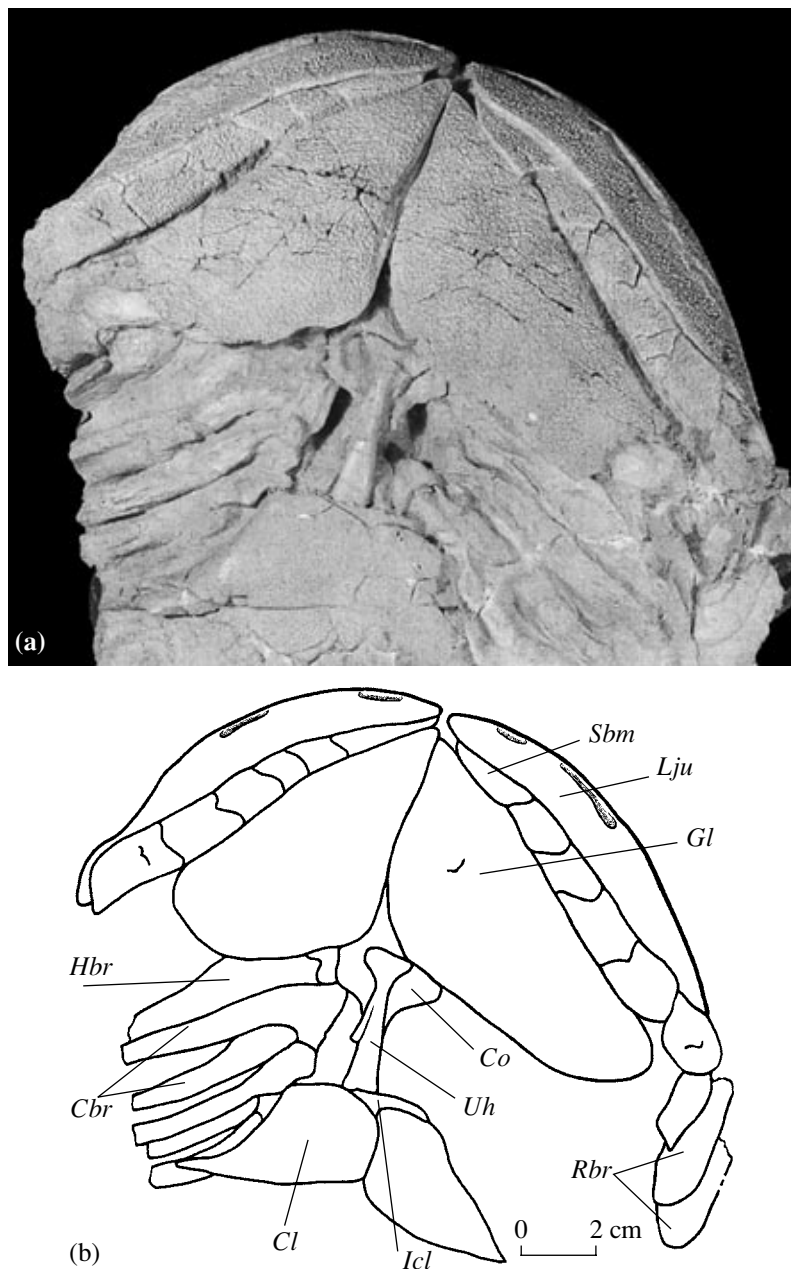
The only naris is positioned dorsolaterally, forming a deep incisure in the anterior region of the shield above the upper jaw at the level of the lacrimal. The anterior margin of the lacrimal has a deep incisure containing the prelacrima (*Pla*), which forms the posterior rim of the naris. In this case, the naris was most likely divided into anterior and posterior parts by soft tissues (Vorobyeva, 1980). The orbits are relatively small, occupy a dorsal position in the skull roof close to the middle of the anterior shield. The distance between them is approximately 1.3 times greater than the length of the shield. The orbital rim is formed by the jugale (*Ju*), which participates in the formation of the posterior and ventral orbital borders; the lacrimale (*La*), which participates in the formation of the ventral and anterior borders; and the postorbitale (*Po*), which along with the supraorbitalia (*So*) forms the dorsal border and, partially, the posterior border.

The width of the posterior shield at the caudal margin is more than twice as great as the shield length. At the posterior margin, each postparietosupratemporal (*PpaSt*), which forms this shield, is 1.4–1.5 times as wide as its width at the anterior margin and the width of the middle part posterior to the lateral projections that border anteriorly the area overlapped by the tabulare (*Ta*). The distance from the line connecting the apices of these projections to the anterior margin of the shield is somewhat shorter than the distance to its posterior margin (the ratio is approximately 1.3). The center of ossification of the parietosupratemporale falls on this line. The tabulare is moderately narrow at the posterior margin; the ratio of the bone length to the width at this margin is approximately 2–2.5. The lateral margin bordered by the extratemporale (*Et*) is slightly concave. The length of the extratemporale at the medial margin is almost 1.5 times greater than its width at the base; the lateral margin of the bone is almost vertical and approximately as long as the medial margin. The surface of the extratemporale is pierced by deep sensory grooves, as that of the tabulare. The extrascapular series displays an overlapping pattern typical of porolepiforms, i.e., the medial extrascapular (*Extm*) overlies the lateral extrascapulars (*Extl*). The rostrocaudal extent of this series is slightly more than half the length of the postparietal shield. The width to length ratio of the lateral extrascapulars is at least 1.3. Medially, these bones closely approach the medial suture of the shield and are considerably overlapped by the medial extrascapular.

The cheek plate is formed of the lacrimal, jugal, postorbital, five squamosals (*Sq*) (in addition to a large upper bone, up to four smaller bones positioned posterovertrally are present), quadratojugal (*Qj*), and preopercle (*Pop*). The lacrimal (*La*) is a relatively small, low, longitudinally extended bone, with a deep incisure in the anterior margin for the prelacrima, a superficial orbital incisure in the posterior part of the upper margin, and a gently sloping posterior margin, which adjoins the jugal. The length of the lacrimal is three times greater than its height at the level of the anterior border of the orbital incisure. The jugale (*Ju*) is high, its height is 1.5 times greater than the length. The jugal is 1.2–1.3 times as long as the lacrimal. The upper margin of the jugal comes in wide contact with the postorbital and the upper squamosal; the anterior margin contains a deep orbital incisure, which forms most of the posterior orbital rim. The posterior margin of the jugal enters an incisure formed by the lower squamosals. The postorbital is longitudinally extended, somewhat shorter than the jugal, reaches the line of the posterior margin of the anterior shield. It forms a small piece of the posterior orbital border and a piece of the upper border. The posterior margin of this bone adjoins the rounded oval prespiracular plate (*Psp*), which is slightly shorter than the bone. The praespiracular enters medially between the parietal and postparietal shields; laterally, it overlies the squamosal (Figs. 1, 2), thus, connecting the roof shields with the cheek plate. This bone lacks a branch of the supraorbital sensory canal (in contrast to that of *Holoptychius*). The length of the upper squamosal is 1.5 times greater than its maximum height at the midline. This bone along with the tabulare, praespiracular, and quadratum form the border of the spiracular incisure (Fig. 1, *sp*). The posterior region of the cheek plate is formed by a large preoperculum (*Pop*), which enters the incisure in the posterior margin of the upper squamosal, which is at most 1.5 times larger than the preopercle. The preopercle is a high, obliquely positioned bone, with the height to length ratio about 1.5. The anterior half of the preopercle is crossed by the preopercular–mandibular sensory canal. The posteroventral corner of the cheek plate is occupied by a low quadratojugale (*Qju*), which comes in contact with the maxilla and one lower squamosal. The cheek plate overlies the low maxilla, the length to height ratio of which is more than 8.

The gill cover consists of a large operculum (*Op*) and suboperculum (*Sop*) (Figs. 1, 2). The operculum is twice as large as the suboperculum, its diagonal length is 1.1–1.3 times greater than the length of the postparietal shield, while the width at the posterior margin is 1.1–1.2 times greater than the length at the medial margin, which adjoins the extrascapulare laterale and the extratemporale.

The dermal cover of the ventral surface of the skull is mostly formed of paired lateral gular plates (gularia lateralia, *Gl*; Fig. 3); while the median gulare is absent. The width of the gularia lateralia at the posterior margin

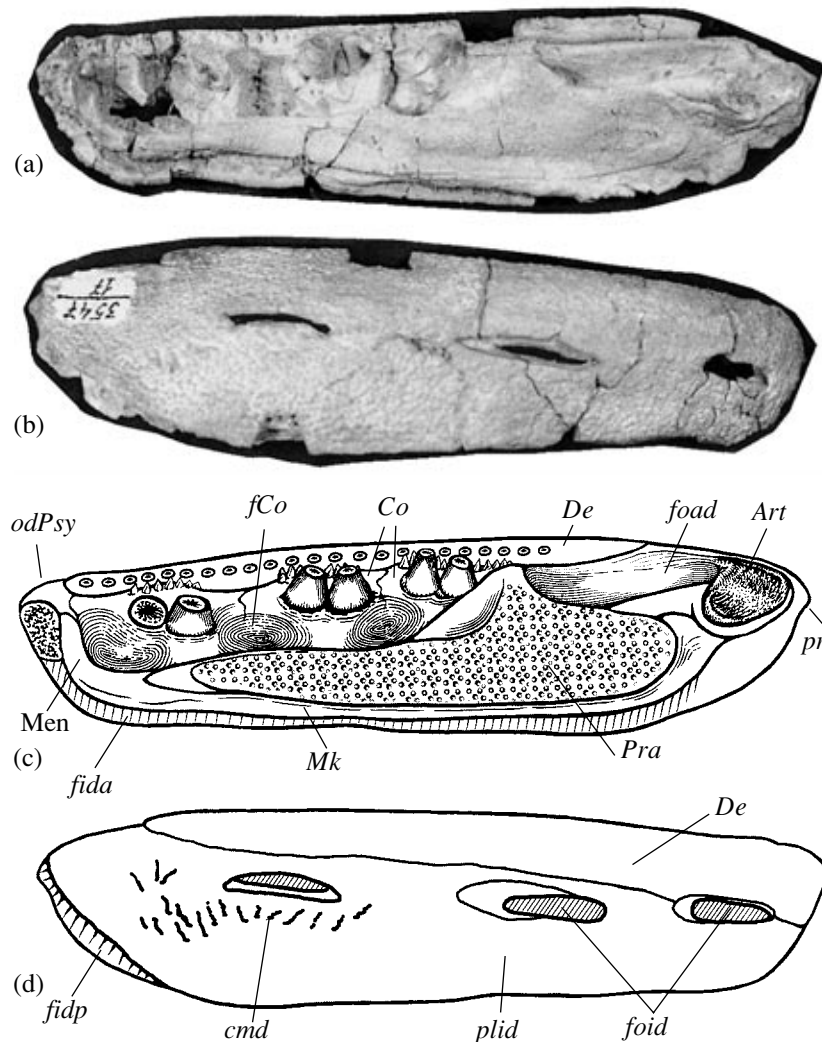


**Fig. 3.** *Laccognathus grossi* sp. nov., holotype PIN, no. 3547/7, skull, ventral view: (a) general appearance and (b) drawing. Designations: (*Cbr*) ceratobranchiale, (*Cl*) clavicula, (*Co*) copula, (*Gl*) gulare laterale, (*Hbr*) hypobranchiale, (*Icl*) interclavicula, (*Sbm*) submandibulare, and (*Uh*) urohyale. For other designations, see Fig. 1.

is approximately the same as its length at the medial margin and half as wide as the lateral margin. The posterior margin of the bone reaches the line of the sixth submandibulare (*Sbm*). The medial margin of some gularia has an area overlapped by its counterpart. The lateral margin has a longitudinally extended area overlapped by the submandibular series, which consists of six bones. This series is terminated by a relatively large bone located on the lateral side of the skull posterior to the palatoquadrate complex and adjoining posteriorly the praeoperculum and quadratojugale–praeoperculo-

submandibulare (*Psbm*). A series of radiobranchialia composed of five elements is located between the gularia lateralia, praeoperculo-submandibulare, and suboperculum.

The lower jaw (Fig. 4) is wide and relatively high, the length to depth ratio is 3.7–4. The jaw is 3.5 times as long as the adductor fossa. The dentary (*De*) is relatively low; at the anterior margin, it is at most one-third of the jaw depth. The anterior end is slightly widened and, anterior to the tooth row, has a small lowered area overlapped by the parasymphysial plate (Fig. 5), which

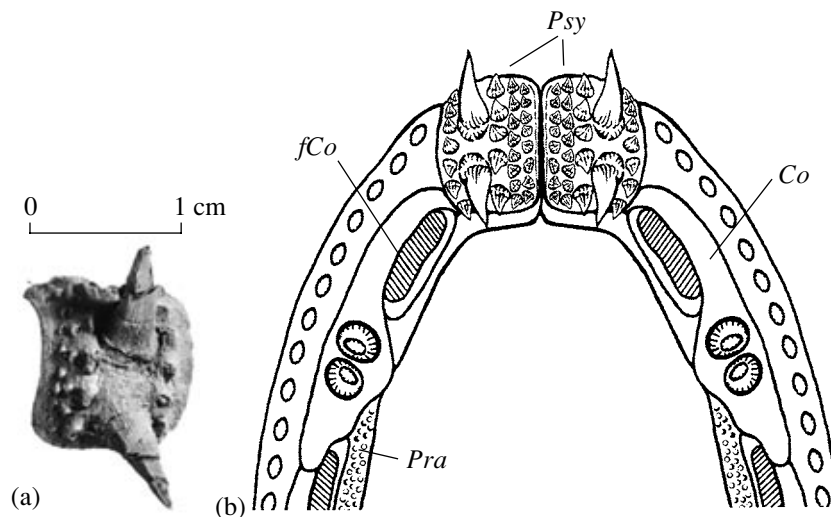


**Fig. 4.** *Laccognathus grossi* sp. nov.: (a, b) specimen PIN no. 3547/17, right ramus of the lower jaw: (a) medial and (b) lateral views; (c, d) reconstruction of (c) medial and (d) lateral surfaces of the lower jaw based on specimens PIN, nos. 3547/17 and 3547/18. Designations: (*Art*) articulare and articular facet for the palatoquadratum, (*Co*) coronoids 1–3, (*cmd*) mandibular sensory canal, (*De*) dentale, (*foia*) infradental incisures and fossae, (*fidp*) posterior infradental flange, (*foad*) adductor fossa, (*Men*) mentomandibulare, (*Mk*) Meckel's bone, (*odPsy*) area overlapped by the parasymphysial plate, (*Pra*) praearticulare, (*plid*) infradental sensory pitted line, and (*pr*) retroarticular process.

is homologous to the adsymphysial plate of osteolepiforms and to the coronoids (Vorobyeva, 1977, 1990). The parasymphysial plate is relatively small, transversely expanded, convex externally, and concave internally. Its anterior and posterior margins are straight, while the lingual and labial margins are slightly concave. The plate has two high, curved caniniform teeth in the central part, which are confined to its labial and lingual margins. Single and double rows of small teeth extend along the anterior and posterior margins of the plate, respectively. A similar parasymphysial plate is present in the collection examined by Gross (no. f. 631); he determined it as “Symphysknochen” (Gross, 1947, pl. 6, fig. 2) and tentatively assigned to *Hamodus lutkevichi* Obruchev. However, Jarvik (1972) believed that it was most similar to the parasymphysial plate of

*Porolepis*. This plate most likely belongs to *L. panderi*. It has three median canines bordered on the sides by rows of small teeth, which are arranged in two lines on one side and in three on the other.

The coronoid series consists of three coronoids (Fig. 4, *Co*), each having a pair of canines separated by deep coronoid fossae, the bottom of which is covered with the geniomandibular and Meckel's bones. The coronoids have rather high toothed vertical plates, which project above the oral margin of the dentary. The coronoid canines have a rounded base and a knifelike apex, slightly decreasing in size in rostrocaudal direction. The largest bone of this series is the precoronoid, which has a long anterior process reaching the posterior margin of the presymphysial area of the dentary. Other two coronoids are approximately equal in size. The



**Fig. 5.** *Laccognathus grossi* sp. nov.: (a) specimen PIN, no. 3547/17a, right parasymphysial plate, dorsal view; (b) reconstruction of the position of the parasymphysial plate in the jaw of specimen PIN, no. 3547/17a. Designations: (*Psy*) parasymphysial plate. For other designations, see Fig. 4.

posterior process of the posterior coronoid is relatively short compared to that of *L. panderi* (Gross, 1941, text-fig. 11A). The precoronoid fossa is bordered anterolaterally by a high ridge of the mentomandibulare, which reaches the articular facet of the symphysis. The external surface of the jaw has three infradental incisures. The anterior incisure located at the boundary between the dentary and the splenial is the shortest; other two are in the infradentalia. The mandibular sensory canal passes high, under the infradental incisures and opens on the surface in short elongated pores–grooves. The angular pitted line is located below the second infradental incisure. The sensory pores extend into the roof of the infradental fossae, which are connected by a vertical central canal to the Meckel's cavity and by a network of canals to the coronoid fossae. The infradental fossae could have performed several functions related to reception, in particular, with electroreception (Vorobyeva, 1992, p. 89). The anterior infradental flange is low, but long, forms a small ventral border of the praearticulare and Meckel's bone, which widely projects ventral to the praearticulare, reaches the level of the third coronoid, and is overlapped by the submandibular series. The praearticulare extends anteriorly from the articulare, closely approaching the anterior end of the lower jaw, and tapers out at the level of the precoronoid fossa. This bone comes in contact with the coronoids to form a high inner wall of the coronoid fossae. The shagreen cover of the praearticulare reaches the line of the precoronoid canines anteriorly; posteriorly, it has a rounded margin. The symphyseal bones connecting the rami of the lower jaw have not been examined. The articulare has a small retroarticular process.

The ventral surface of the ethmoid has relatively shallow, longitudinally extended palatine fossae, which are separated by a relatively low and narrow medial eth-

moidal projection of the neurocranium (Fig. 6). Anteriorly, the fossae are bordered by a narrow palatine plate of the rostromaxillaria; laterally, they are bordered by wide, short vomers with two canines each. The toothed vertical plate of the vomers slightly projects above the toothed margin of the upper jaw. The lateral margin of the horizontal plate of the vomer has a natural notch, which could have corresponded to the incisure of the exochoana. Anteriorly, the parasphenoid reaches the ethmoidal projection. It has a triangular toothed plate with a sharp apex, which closely approaches the line of the posterior margin of the vomers.

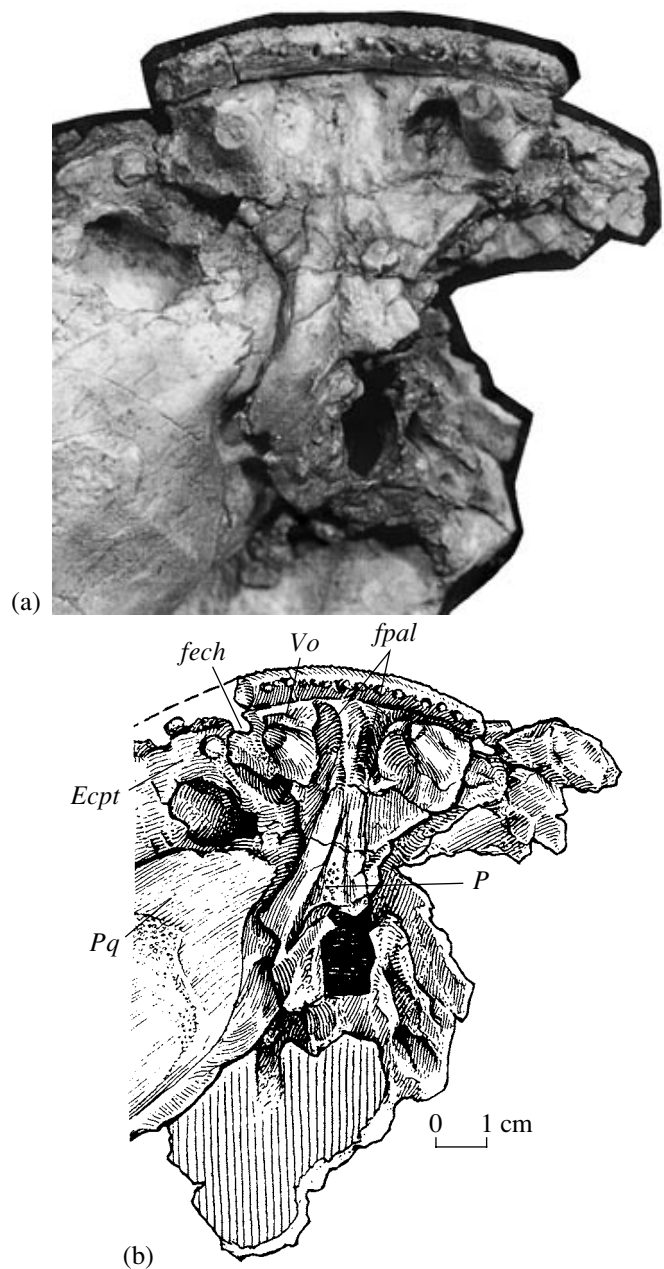
The palatoquadratum (Fig. 6, *Pq*), like that of other porolepiforms and osteolepiforms, is a single bone composed of two major parts, namely, the anterior pars autopalatina and the posterodorsal marginal part with an ascending process. The autopalatine part forms two articulations in the regions of the ethmoidal process and anteromedial plate. The shagreen plate of the entopterygoid reaches anteriorly the line of the anterior ectopterygoid canines. The entopterygoid crest is well developed and forms a wide medial projection. The posterior ramus of the palatoquadratum is moderately developed, forming a relatively wide incisure (which corresponds to the adductor fossa) in the upper half of the jaw apparatus. At the level of the prespiracular plate and upper squamosal, the medial margin of the palatoquadratum has a smooth notch corresponding to the spiracular incisure.

The hyomandibula is a massive, longitudinally extended rod-shaped bone, which adjoins the posterior margin of the palatoquadratum. The proximal end of the bone is widened and has two heads articulated with the braincase. Its distal end tapers out; it was probably connected to the symplecticum, which was covered exter-

nally by the preoperculo-submandibulare, as in *Glyptolepis* and other porolepiforms (Jarvik, 1972, 1980).

The hyobranchial apparatus (Fig. 7) displays a pattern typical of porolepiforms. The basibranchial series is a single rounded element, the width of which is greater than the length. The hyoid arch and three anterior branchial arches are articulated with this element. The anterior margin of the basibranchial has incisures for the hypohyalia (*Hh*), while the lateral margins have three small depressions for articulation with hypobranchials I–III (*Hbr*). The distal end of each of three anterior hyobranchials is articulated with ceratobranchials I–III. Ceratobranchial III provides attachment for ceratobranchial IV, while ceratobranchial V is attached to ceratobranchial IV. The hypohyals are short elements, each side of which has an attachment area for a massive and wide ceratohyal (*Ch*). The ventral surface of the basibranchial is overlapped by the urohyal (*Uh*), a longitudinally extended, rod-shaped bone bifurcating at the distal end, which represents the subbranchial series. The sublingual rod, which is characteristic of osteolepiforms, is absent, as in *Glyptolepis* (Jarvik, 1972, 1980).

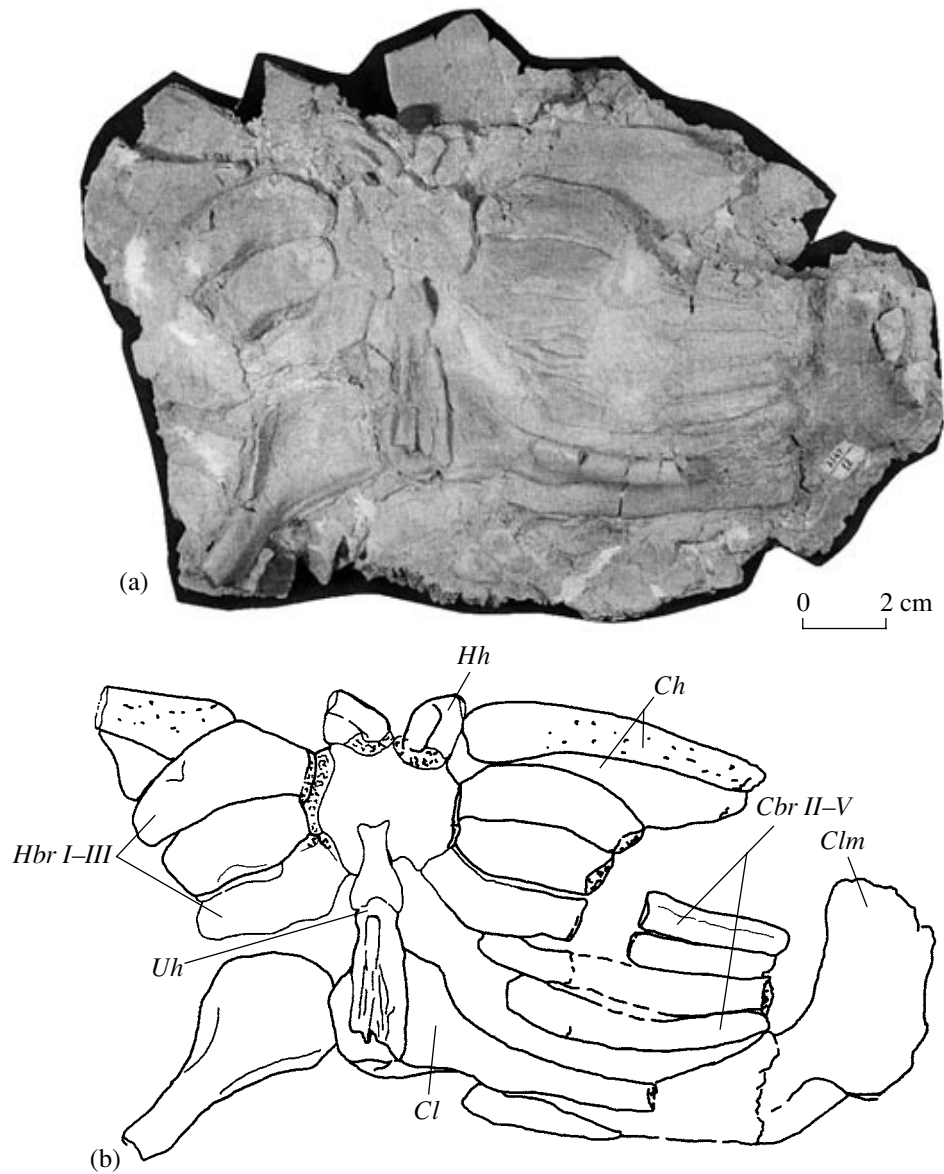
The pectoral girdle is composed of the cleithrum, clavicle, scale-shaped posttemporale, supracleithrum, and anocleithrum. The interclavicle (Fig. 8, *Icl*) is for the first time recorded with certainty in porolepiforms; it is a short, wide bone with scalloped posterior and lateral margins and a small and low medial crest, which expands anteriorly to form an elevated anterior margin covered with ornamentation of denticles. The denticles are hardly discernible on the edge of the crest, which probably separated the clavicles, which, as they overlapped each other, rested against the anterior elevated margin of the interclavicle. The collection examined by Gross contains a bone that he characterized as “an indeterminate sculptureless median bony plate probably belonging to *Dipterus ? crassus*” (Gross, 1936, text-fig. 7H), which is similar in shape to the interclavicle of *L. grossi*. This is probably a considerably rounded interclavicle of *L. panderi*. The cleithrum (Fig. 7) has a relatively short vertical ramus, which is approximately 0.83 as long as the horizontal ramus (or, sometimes, they are equal in length). Both rami are located within the same plane. The upper and anterior margins of the internal surface of the horizontal ramus have lowered areas overlapped by the clavicle. The clavicle is typical in structure for porolepiforms; its anterior part is widened, slightly arched, while the ascending process is long, rod-shaped, covered by the cleithrum. This rod-shaped part varies in length; sometimes, the widened part is almost 1.5 times as long as the rod-shaped part. The external surface of the cleithrum and the widened plate of the clavicle are covered with denticles, except for the anterior margin of the cleithrum, which has a smooth area overlapped by the gill cover. This area extends onto the clavicle and tapers out in its anterior part. The ascending process of the clavicle has a short basal expansion, pronounced to a greater or lesser extent, which sometimes has serrated margins representing a



**Fig. 6.** *Laccognathus grossi* sp. nov., specimen PIN, no. 3547/5, palatal surface of the ethmoid and the anterior part of the palatoquadrate complex: (a) general appearance and (b) drawing. Designations: (*Ecpt*) ectopterygoid, (*fch*) incisure of the choana, (*fpal*) palatine fossa, (*P*) parasphenoid, (*Pq*) palatoquadrate, and (*Vo*) vomer.

nonsculptured projection at the median margin of the bone. This projection probably participates in the formation of the posterior wall of the branchial cavity.

The skeleton of fins and vertebral column is poorly understood. In the anterior dorsal fin, the lepidotrichia are whole, bifurcating in placed, attached to the elongated basal plate; one plate is at the base of the first dorsal and anal fins and three or four are at the base of the

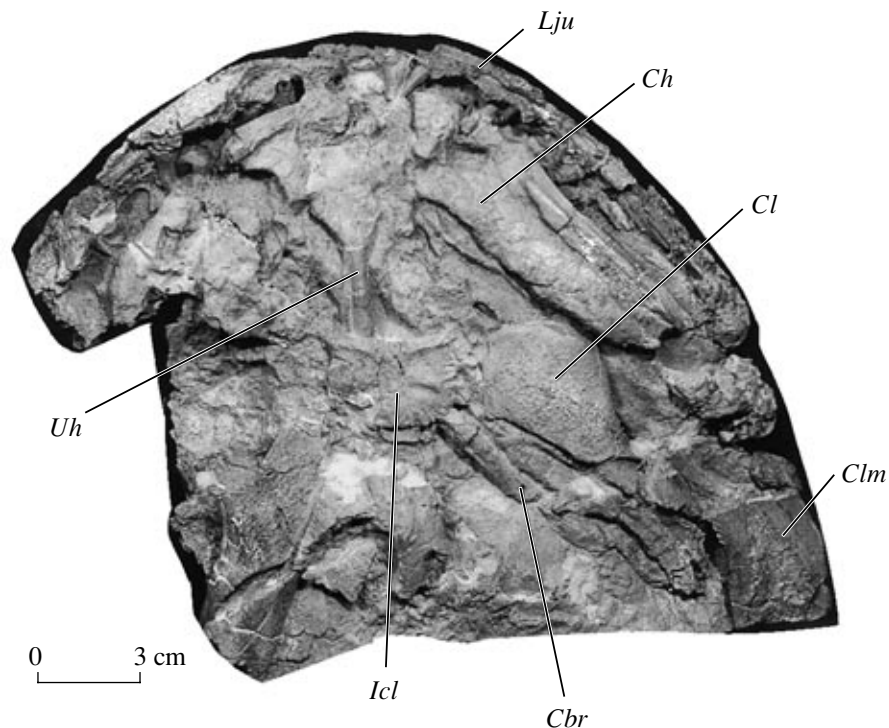


**Fig. 7.** *Laccognathus grossi* sp. nov., specimen PIN, no. 3547/12, hyobranchial apparatus and clavicles, ventral view: (a) general appearance and (b) drawing. Designations: (*Ch*) ceratohyale and (*Hh*) hypohyale. For other designations, see Fig. 3.

second dorsal fin. The dorsal and anal fins are positioned relatively close to the caudal fin. The caudal fin is heterocercal, with a low, long epichordal blade and a rounded hypochordal blade, which is three times as wide as the upper blade. The pectoral fins are wide and relatively short (in a fish with a 100-cm-long body, they are 8–10 cm long and 7 cm wide), the fleshy lobe is narrow, and the lepidotrichia are long. The abdominal fins are of the same size. The pectoral fin has a biserial skeleton. The fleshy lobes of paired fins are medium-sized. The ossified pleurocenters and intercenters are observed in the pectoral region, while the caudal region has ossified neural and haemal arches. The scales are massive, rounded, widely overlapping each other, ornamented with cupola-shaped denticles, under which the

earlier generations of denticles are recognized. The canal of the lateral line is in the shape of an open groove with short, branching grooves diverging from it. The teeth display a typical dendrodont microstructure.

**Measurements** in cm. Specimen PIN, no. 3547/30 (in the right posterior corner of the monolith): fish length, 120; skull width between posterior margins of the lower jaw, 44; skull length from the anterior margin of the snout to the posterior margin of the gularia laterale, 22; specimen PIN, no. 3547/31 (in the anterior part of the monolith): fish length, 100; the origin of the pectoral fins is at a distance of 30 cm from the anterior edge of the snout; abdominal fin length, 62; lower jaw length, 7; gularia laterale, 13; holotype PIN, no. 3547/7:



**Fig. 8.** *Laccognathus grossi* sp. nov., specimen PIN, no. 3547/24, skull, ventral view, with gularia removed; a part of the hyobranchial apparatus and external sides of the clavicular and interclavicular are visible. For designations, see Figs. 1, 3, and 7.

skull length from the anterior edge of the snout to the posterior margin of the extrascapular medialis, 16; specimen PIN, no. 3547/6: lower jaw length, 9.8; specimen PIN, no. 3547/5: length of the palatoquadrate complex, 15; specimen PIN, no. 3547/8: length of the horizontal and vertical rami of the cleithrum, 10 and 6.5, respectively; specimen PIN, no. 3547/15: clavicle length, 12.5; length of the ascending process, 7; specimen PIN, no. 3547/24: length of the parietal shield, 5.5; and length of the postparietal shield, 6.7.

**Comparison.** Available specimens of *L. panderi* are rather fragmentary; therefore, only a few characters can be compared with the new species, which is represented by complete skulls and almost complete fishes. However, they are quite enough to validate the new species, *L. grossi*. This species differs from *L. panderi* in the smaller orbit, which occupies a more dorsal position (judging from the incisure in the jugal). The shape and proportions of the postparietal shield and some bones of the skull roof are also different. In *L. grossi*, the postparietal shield is relatively wider at the posterior margin, while the suprapostparietal is relatively narrower in the middle part (just posterior to the lateral projection). *L. grossi* has a wider extratemporal, a narrower anterior margin of the tabular, which is almost rectangular in outline; the extrascapular series is shorter, and the lateral extrascapulars are wider and considerably overlapped by the medial extrascapular. The ratio between the parietal and postparietal shields of *L. panderi* remains the same; however, the parietoin-

tertemporal is probably longer, at least 0.4 times as long as the postparietal shield (in *L. grossi*, this ratio is almost 0.33). In *L. panderi*, the postrostral series wedges in between the parietointertemporalia to a lesser extent and terminates short of the midlength of these bones and the lateral branch of the supraorbital canal. The holotype of *L. panderi* is a lower jaw (Gross, 1942), which is clearly lower than the jaw of *L. grossi*; the length to depth ratio is 5, while in *L. grossi*, it is 3.7–4. The lower jaw of a small individual (PIN, no. 3547/17) allows a detailed comparison with *L. panderi*. The total length of its jaw is 17.5 cm, the greatest depth at the posterior infradental incisure is 4.4 cm. The adductor fossa, the anterior border of which is in line with the anterior margin of this incisure, is 4.6 cm long. Thus, the jaw length is 4 times greater than the depth and almost 4 times (3.8) greater than the length of the adductor fossa (in *L. panderi*, these ratios are 5 and no more than 3.3). In either species, the prearticular reaches anteriorly the line of the precoronoid fossa, while its shagreen cover reaches the line of the second precoronoid canine. Posteriorly, this cover is rounded in outline at the level of the posterior third of the adductor fossa (in *L. panderi*, this character has not been recorded, probably, in connection with incomplete preservation of available jaws). In either species, the precoronoid process is long, reaches the smooth-walled area on the upper margin of the dentary, which is overlain by the parasymphysial plate. The vertical plates of the coronoids of *L. grossi* are relatively higher, project

above the toothed margin of the dentary. The mentomandibulare, which covers the bottom of the precoronoid fossa, forms a relatively high, rodlike medial wall of this fossa, a natural continuation of the anterior rodlike end of the praearticulare, in contrast to that of *L. panderi*. The posterior coronoid process of *L. grossi* is relatively shorter than that of *L. panderi*.

In *L. panderi*, the medial row on the presumable parasymphysial plate is composed of three canines (versus two in *L. grossi*, Fig. 5), while the rows of small teeth bordering them at the edges consist of two anterior (one in *L. grossi*) and three posterior (two in *L. grossi*) rows. The two species also differ in postcranial skeleton. The cleithrum has a relatively shorter vertical ramus (in *L. panderi*, the ratio of these rami is 1 : 1. The ascending process of the clavicle is relatively shorter and twisting to a lesser extent, the apex of the process is located in the horizontal plane (compare with Gross, 1936, text-figs. 3A–3E, where the clavicle is mistakenly designated as the pterygoideum).

**Material.** Four almost complete fish skeletons, three well-preserved skulls, and about 30 fragments, including three lower jaws, several hyobranchial apparatuses, an incomplete ethmosphenoid, postcranial bones, scales, and teeth from the type locality (specimens PIN, nos. 3547/5–35).

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