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Source: *Acta Palaeontologica Polonica*, 61(4) : 829-838

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00247.2016>

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Cenozoic fossil fishes of the extinct alepisauroid family Polymerichthyidae from the Sakhalin Island, Russia

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Nazarkin, M.V. 2016. Cenozoic fossil fishes of the extinct alepisauroid family Polymerichthyidae from the Sakhalin Island, Russia. *Acta Palaeontologica Polonica* 61 (4): 829–838.

Five incomplete skeletons of fishes of the extinct monotypic family Polymerichthyidae (Aulopiformes: Alepisauroidei) from the Paleogene and Neogene of Sakhalin Island, Russia, are identified as *Polymerichthys* sp., described in detail, and compared with known representatives of the family. The results of this study suggest that polymerichthyids were characterized by a prolonged rostrum, behind which the upper jaw symphysis was placed; by an anal fin without spinules, contrary to what was assumed earlier; and, probably, by sexual dimorphism. Morphological analysis reveals the closest relationships of Polymerichthyidae to be with Recent Alepisauridae, but their taxonomic position is still unresolved. The new material is the second occurrence of articulated skeleton of fishes of this family. The new findings from Sakhalin expand the known geographical distribution of Pacific polymerichthyids by about 12° of latitude, and extend the time interval for this family to as early as the late Oligocene.

Key words: Teleostei, Aulopiformes, *Polymerichthys*, morphological analysis, systematics, Tertiary, Russia, Sakhalin.

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Received 4 February 2016, accepted 29 April 2016, available online 10 May 2016.

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Introduction

The monotypic family Polymerichthyidae was established for the morphologically unusual alepisauroid fish *Polymerichthys nagurai* Uyeno, 1967, discovered in the Miocene sediments of Japan (Uyeno 1967). Polymerichthyidae are one of the six extinct families of teleosteans that inhabited the North Pacific in the Neogene, along with the anguilliform family Deprandidae, the beloniform family Forficidae, the perciform families Ioscionidae and Euzaphlegidae (all known from the Miocene of California, USA) and the trachiniform family Trispinacidae (described from Serravalian of Sakhalin Island, Russia) (Jordan and Gilbert 1919, Jordan 1924; David 1943; Danil'chenko 1960; Nazarkin 2002; Fierstine et al. 2012).

Polymerichthyidae show a certain similarity with the Recent Anotopteridae in having: slender elongated body; comparatively large head, pointed anteriorly and flattened laterally; ventral position of pectoral fin; greatly elongated ribs and intermuscular bones; palatine bearing largest teeth of mouth gape; and large saber-like and anteriorly inclined palatine teeth. The last character is not found anywhere among other Teleostei. Fossil Polymerichthyidae differ from the Recent anotopterids in having: long-based dorsal fin (absent in Anotopteridae), numerous vertebrae (~186 vs. 76–85) (Rofen 1966; Iwami and Takahashi 1992; Kukuev

1998), and much reduced caudal fin. The structure of the anal fin of *Polymerichthys nagurai* was thought to be similar to those of recent deep-sea eels of the genus *Nemichthys* (Anguilliformes: Nemichthyidae) in that the first 28 anal fin rays look like short paired spinules (Uyeno 1967).

The only known specimen, the holotype of *P. nagurai*, came from the Middle Miocene beds of the Tubozawa Formation, Horaiji, Aichi Prefecture, Japan (Uyeno 1967; Yabumoto and Uyeno 1994). Since the initial description, only an isolated toothed palatine of *Polymerichthys* sp. has been reported from the Middle Miocene (Serravalian) of Italy (Carnevale 2007). In the present paper, the discovery of five partial skeletons of *Polymerichthys* sp. in the upper Oligocene Holmsk Formation and the Middle–Upper Miocene Kurasi Formation of Sakhalin Island, Russia, are reported. These new specimens provide new information on the morphology of this enigmatic extinct family, and on its geographic and stratigraphic distribution. The detailed description of this material, accompanied by comparative analysis and discussion of the taxonomic position of the Polymerichthyidae, follows.

Institutional abbreviations.—NSMT, National Museum of Nature and Science, Tsukuba, Japan; ZIN, ichthyological collection, Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia.

Geological setting, material, and methods

Specimens were collected on the south-western side of Sakhalin Island at the coastal cliffs of the Tartar Strait, which are located in the Tomari District of Sakhalin Province, Russia (Fig. 1). Two articulated partial skeletons were discovered in the fossiliferous beds of the upper Oligocene Holmsk Formation and three skeletons in the Middle–Upper Miocene Kurasi Formation. At the Tomari District, the Holmsk Formation is represented by clayish, tuffaceous and siliceous aleurolite, whereas the Kurasi Formation typically comprises gaize, diatomite siltstone, and tuffaceous diatomite (Savitskiy 1982; Zhidkova 1982, 1986; Gladenkov et al. 2002). These formations were deposited during periods of extensive Cenozoic marine transgressions. In the deposits of both formations, complexes of deep-water and neritic fishes, with a predominance of myctophids, were discovered (Nazarkin 2012, 2014, 2015; Nazarkin and Bannikov 2014).

The fossiliferous outcrop of the Kurasi Formation is a coastal cliff of Tartar Strait, located about 5 km south of the settlement of Penzenskoye and about 7 km north of the settlement of Nevodskoye. The Holmsk Formation outcrop is located 1 km south of the settlement of Nevodskoye and 3 km north of Tomari city (Fig. 1).

The matrix was removed by needles under a stereomicroscope. The measurements were taken by a vernier caliper to within 0.1 mm. The drawings were made according to digital photographs, and based on both the part and the counterpart of the specimens. The osteology of Recent fishes, used for comparison, was studied by radiographs and one cleared and stained specimen of *Anotopterus vorax* (Regan, 1913) ZIN 42069. Comparative material included *Alepisaurus brevirostris* Gibbs, 1960, ZIN 38283; *Alepisaurus ferox* Lowe, 1833, ZIN 45268; *Anotopterus vorax*, ZIN 42069, ZIN 41799; and *Polymerichthys nagurai* Uyeno, 1967, holotype, NSMT PV 6599.

Systematic palaeontology

Class Actinopterygii

Division Teleostei

Subdivision Euteleostei

Order Aulopiformes

Suborder Alepisauroides sensu Davis, 2010

Superfamily Alepisauroidea sensu Davis, 2010

Family Polymerichthyidae Uyeno, 1967

Genus *Polymerichthys* Uyeno, 1967

Type species: Polymerichthys nagurai Uyeno, 1967; Middle Miocene, Tubozawa Formation, Horaiji, Aichi Prefecture, Japan.

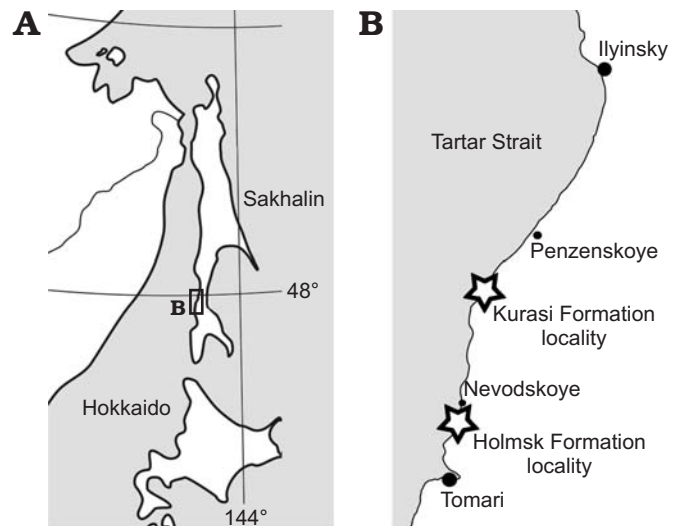


Fig. 1. Location of the Sakhalin Island (A) and sketch map of the studied area (B) showing the fossil fish localities (stars).

Stratigraphic and geographic range.—Late Oligocene–Late Miocene, Northwestern Pacific.

Polymerichthys sp.

Figs. 2–5.

Material.—ZIN 310p, partial skeleton in part and counterpart (neurocranium length ~62.4 mm); ZIN 311p, partial skeleton in part and counterpart (neurocranium length 81.2 mm); both from Holmsk Formation, late Oligocene. ZIN 312p, partial skeleton (neurocranium length 93.8 mm); ZIN 313p, incomplete head (neurocranium length ~80 mm); ZIN 314p, partial skeleton in part and counterpart (neurocranium length 71.5 mm); all from Kurasi Formation, Middle–Late Miocene.

Specimen ZIN 313p represents only the anterior part of the head, whereas the others are partial skeletons with the head almost complete, and the anterior part of the axial skeleton, including abdominal vertebrae, elements of the dorsal fin (ZIN 312p and ZIN 314p), and of the pectoral girdle (ZIN 310p and ZIN 314p) well preserved (Fig. 2).

Measurements.—Measurements of the studied specimens are shown in Table 1. The standard lengths of specimens from Sakhalin, estimated from the proportion of the tallest palatine tooth with that of the holotype of *P. nagurai*, is 312.0 mm for ZIN 310p; 257.6 mm for ZIN 311p; 244.9 mm for ZIN 312p; 198.4 mm for ZIN 313p; and 270.2 mm for ZIN 314p.

Description.—The body is greatly elongated, slender, and eel-like (Figs. 2–4). The head is large narrowed anteriorly, wedge-shaped, and, probably, laterally compressed. The greatest height of the head is at the mandibular joint. The snout is long, thin and pointed. The snout length is approximately 75% of the neurocranium length. The eyes are lateral in position. The orbit length is 10.5–10.6% of neurocranium length.

The bones of the cranium and visceral skeleton lack any traces of superficial ridges or tubercles. The neurocranium

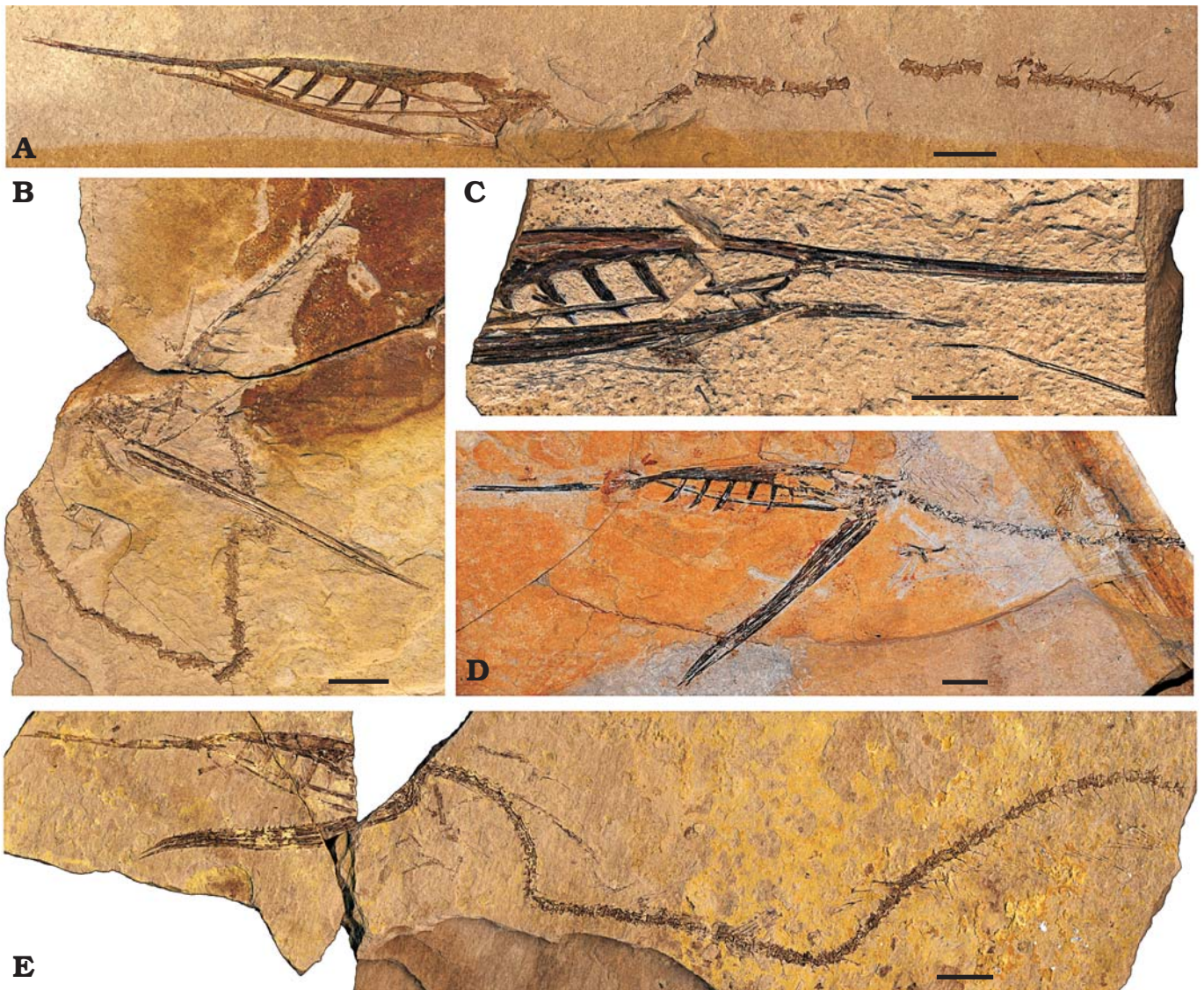


Fig. 2. Alepisauroid fish *Polymerichthys* sp. from Sakhalin Island, Holmsk Formation, late Oligocene (A, B) and Kurasi Formation, Middle–Late Miocene (C–E). A. ZIN 311p. B. ZIN 310p. C. ZIN 313p. D. ZIN 312p. E. ZIN 314p. Scale bars 10 mm.

is long, narrow, and wedge-shaped. The orbito-rostral part of the neurocranium is 5.7–6.2 times longer than the cranial part. The shapes and borders of cranial bones are mostly unclear. The skull roof is formed mainly by the frontals, which are the longest cranial bones. They are thin and tightly joined to each other. The lateral edges of the frontal do not form any prominent projections above the orbit, and bear weak porous sculpture (ZIN 311p; Fig. 3D). The frontals are prolonged anteriorly, significantly anterior to the anterior palatine tooth, forming a sharp rostrum. The anterior end of the frontals bears a sharply pointed antero-ventral projection, (Figs. 2, 3). Any traces of other snout ossifications, which could be a part of the rostrum, are not recognizable.

A prominent knob is located on the ventral surface of the neurocranium ahead the midpoint of its length (Figs. 3, 4). This knob, apparently, represents the vomerine head. Its edge is serrated, and it sometimes bears 1–3 small teeth (ZIN 311p, 313p, 314p; Fig. 3B–D). “Vomerine” teeth are

conical, sharp and of moderate size (longer than premaxillary teeth but shorter than dentary teeth). The base of these teeth is not ossified posteriorly (Fig. 4B). Thus, they can be considered as depressible teeth of the third or fourth type (Fink 1981).

At the posterior part of the neurocranium of specimens ZIN 311p and ZIN 312p there are paired triangular elements, extending posteriorly and close together. Probably, they are the parietals, which were displaced from their true position (Figs. 2, 3). The parasphenoid is thin and slightly curved ventrally under the anterior margin of the orbit (Fig. 3D). Other bones of the neurocranium are indistinguishable on the studied specimens.

The joint of the lower jaw is located posterior to the orbit. The boundaries of the lower jaw bones are not distinguishable. The lower jaw is thin and very long, approximately 15–20 times as long as its greatest height at the coronoid process. Usually, the mandible is significantly shorter than the

Table 1. Measurements (in mm) of the specimens of *Polymerichthys* sp. from the Cenozoic of Sakhalin.

Specimen	ZIN 310p	ZIN 311p	ZIN 312p	ZIN 313p	ZIN 314p
Neurocranium length	~62.4	81.2	93.8	~80.0	71.5
Neurocranium height	4.9	5.3	6.1	–	6.3
Snout tip to quadrate head length	59.2	80.4	91.5	–	70.3
Orbit length	–	10.3	10.0	–	–
Mandible length	57.3	58.2	58.5	–	53.8
Coronoid process height	2.9	>2.1	3.7	–	>4.4
Mandible teeth height	2.2	1.9	2.6	2.0	1.5
Upper jaw length	–	67.0	73.4	–	57.2
Upper jaw teeth height	–	0.2	0.5	0.4–1.0	0.6–1.8
Length of 10 abdominal vertebrae	26.4	33.8	37.8	–	25.8
First palatine tooth height	>6.4	>6.4	7.7	~6.0	6.0
First palatine tooth base width	1.3	1.3	1.4	1.3	1.0
Second palatine tooth height	>7.5	>7.5	8.2	7.0	7.0
Second palatine tooth base width	1.3	1.3	1.4	1.5	1.1
Third palatine tooth height	>7.7	>7.7	8.7	6.7	~7.0
Third palatine tooth base width	1.3	1.3	1.5	1.5	1.1
Fourth palatine tooth height	7.3	7.3	8.4	~6.6	6.2
Fourth palatine tooth base width	1.2	1.2	1.6	1.4	1.0
Fifth palatine tooth height	5.3	5.3	7.1	~3.5	3.7
Fifth palatine tooth base width	1.2	1.2	1.3	1.0	0.7
Sixth palatine tooth height	absent	absent	3.3	absent	absent
Sixth palatine tooth base width	absent	absent	1.1	absent	absent
Seventh palatine tooth height	absent	absent	1.5	absent	absent
Seventh palatine tooth base width	absent	absent	0.8	absent	absent

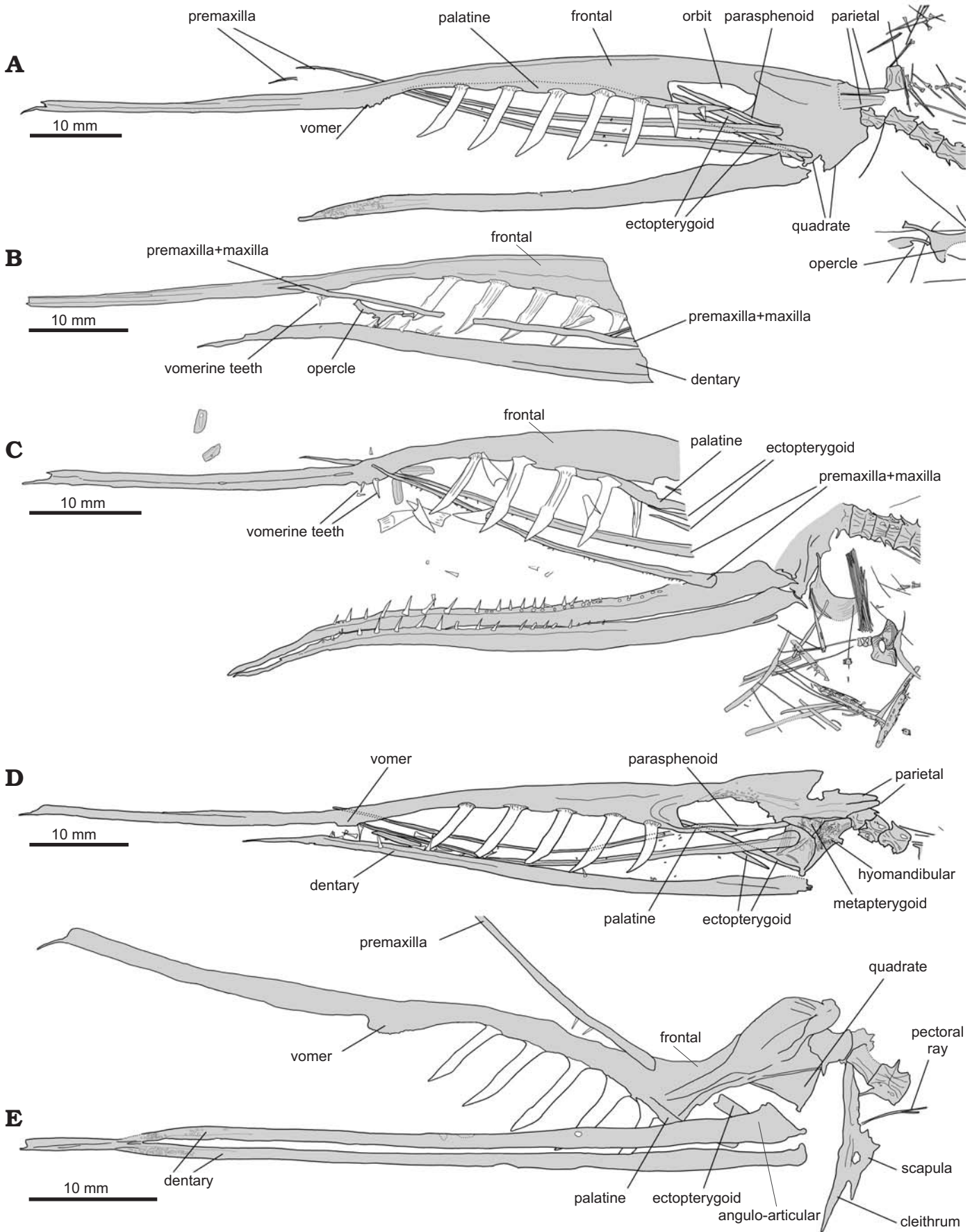
head; its anterior edge reaches slightly anterior to the “vomere” knob (Fig. 3A–D) and its length is 59.5–73.0% of the neurocranium length. However, in ZIN 310p the mandible almost reaches the anterior end of the snout, and its length is about 91.9% of the neurocranium length. The mandible length, expressed as the distance between the four anterior palatine teeth, is between 3.2 and 3.9, except for ZIN 310p in which this proportion equals 4.9. A spur-like process on the posterior edge of the mandible, arising, probably, from the retroarticular, can be seen in the best-preserved specimen (ZIN 314p, Fig. 4). The anteriormost parts of the dentary are thin, medially jointed, without teeth, and bearing porous sculpture on their surface. They gradually narrow anteriorly and form pointed projections. The lower jaw teeth are sharp, thin, and straight, of the first type (Fink 1981). They appear to be arranged in one row, in a position perpendicular to the mandible, or sometimes slightly inclined posteriorly. The tooth crowns are flattened laterally, with two sharp cutting edges. The tallest teeth are located at the anterior one third of the tooth row; anteriorly and posteriorly from this area tooth height is gradually reduced (Fig. 4B).

The premaxilla and maxilla are long and thin, very closely adjacent to each other, so that the border between them is often indistinguishable. Ascending and articular processes of the premaxilla are, apparently, absent. The

anterior edge of the premaxilla is thin, pointed, without premaxillary fenestra, and placed considerably far behind the anterior end of the snout. In most of the specimens, the anterior parts of the premaxillae are visible above the skull slightly ahead of the “vomere” knob (Figs. 2, 3). The posterior edge of the upper jaw (joined maxilla and premaxilla) is slightly expanded and placed behind the orbit, above the mandible joint (Fig. 3A, C, D). Along almost its entire length the premaxilla bears sharp, slender, and small teeth (the smallest among the mouth gape teeth), arranged, apparently, in one row (Fig. 4B). The height of the upper jaw teeth usually did not exceed the height of the premaxilla, but in ZIN 310p these teeth are taller than the thickness of the premaxilla (Fig. 3E). The maxilla is excluded from the mouth and is toothless. Supramaxillae are, apparently, absent.

The suspensorium is not much inclined, being roughly perpendicular to the longitudinal axis of the neurocranium. Of the suspensorium, the ventral part of a fan-shaped quadrate can be recognized in the most specimens. The posterior part of the hyomandibula, bearing the prominent opercular process, and the flat triangular metapterygoid are discernible in ZIN 311p (Fig. 3D). The ectopterygoids are preserved on most specimens. They are toothless, flat, and elongated bones, inclined posteriorly, where they are connected to the entire anterior edge of the quadrate (Fig. 3A,

Fig. 3. Skulls of alepisauroid fish *Polymerichthys* sp. from Sakhalin Island, Kurasi Formation, Middle–Late Miocene (A–C) and Holmsk Formation, late Oligocene (D, E). A. ZIN 312p. B. ZIN 313p (flipped horizontally). C. ZIN 314p. D. ZIN 311p. E. ZIN310p (flipped horizontally). Lower jaws are brought to the skull in A and E. →



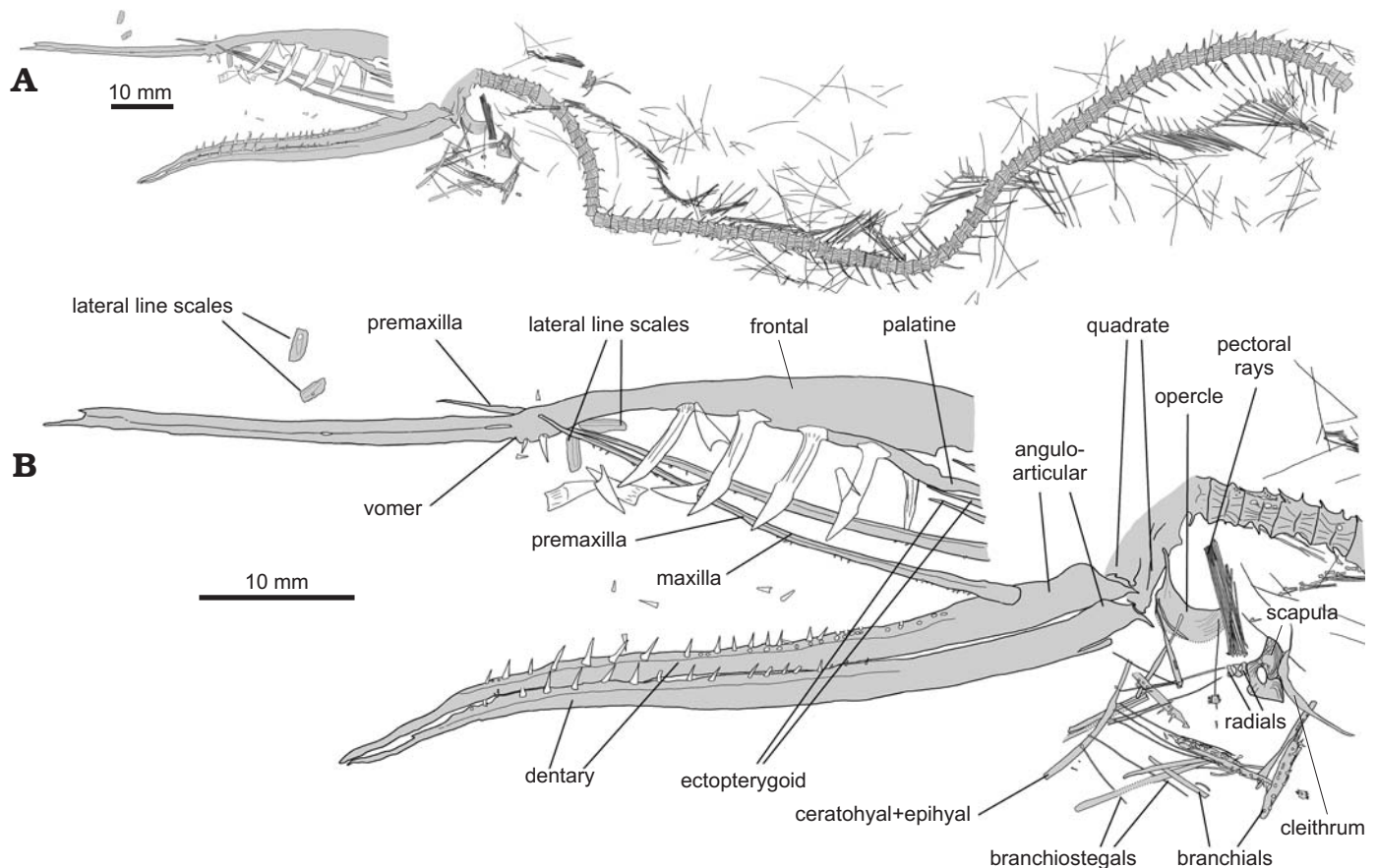


Fig. 4. Alepisauroid fish *Polymerichthys* sp. from Sakhalin Island, Kurasi Formation, Middle-Late Miocene, ZIN 314p, outline drawing of specimen (A) and skull (B).

D). The entopterygoids are not discernible. There are no traces of entopterygoid teeth. The palatines are more than twice as long as the longest palatine tooth. These bones are tightly adjoined to the ventral surface of the neurocranium, and, therefore, their outlines are hard to define. The posterior end of the palatine is slightly inclined postero-ventrally, and loosely attached to the ectopterygoid, such that the bones are disconnected in most skeletons studied (Fig. 3). Along the ventral margin of palatines, there is a united (from the left and right bones) row of five to seven enormously large, saber-like teeth. The second and third, or the second to fourth teeth are the largest (Table 1). The length of the largest palatine tooth is 1.1–1.3 times of the orbit length. The shortest teeth are placed caudally. All palatine teeth are flat, laterally compressed, slightly curved and inclined anteriorly, with two (anterior and posterior) smooth, sharp cutting edges on their crowns. The tips of the crowns of most of the palatine teeth are slightly expanded and lanceolate (Fig. 4B). These teeth are fully ankylosed to the bone (type 1 tooth attachment sensu Fink 1981). Tooth bases are fully mineralized, proximally expanded, and sculptured with short vertical ridges and grooves. Six partially ossified replacement palatine teeth are seen under the neurocranium of ZIN 314p (Figs. 2E, 4B).

The bones of the opercular series are mostly lost. In ZIN 312p, 313p, and 314p a small winged bone, probably the

opercle, is present. This bone is characterized by long and slender anterior part (articular process), and a wide posterior part, divided in larger upper and smaller lower lobes (Fig. 3A–C). The bones of the gill arches are fragmented and largely incomplete. Jointed ceratohyal and epihyal form a thin rod placed postero-ventral to the mandible in ZIN 314p (Fig. 4B). The border between these bones is indiscernible. At least 9 needle-like branchiostegal rays are placed around these bones; 7 of them seem to be attached to this structure. About a dozen unidentifiable branchial bones are seen ventral to the opercle of the same specimen (Fig. 4B). Among them, 6 bones bear at least 1 row of small, conical, slightly curved teeth, which may be modified gill rakers.

The elements of the postcranial skeleton are only partially preserved in the specimens studied. The caudal vertebrae, anal and caudal fins are completely lost. Nineteen abdominal vertebrae are preserved in ZIN 312p, 31 in ZIN 311p, 48 in ZIN 310p, and 63 in ZIN 314p. The first abdominal centrum cannot be discerned. Abdominal vertebral centra are symmetrical and moderately elongated. The height of each centrum is approximately three times less than the length. The neural arches are fused with the centra and closed, with a prominent neural spine. The neural spines are gradually elongated posteriorly; their length is up to three times more than the centrum length. Neural arches are perforated by several (2–5) roundish openings; the largest of them is located

directly behind the base of a neural spine (Fig. 5A). All vertebrae have triangular parapophyses, also slightly elongated posteriorly. Triangular pre- and postzygapophyses are discernible on some vertebrae. Vertebral centra are ornamented by 4–6 longitudinal striae. In addition, a prominent vertical crest extends from the dorsal edge of a parapophysis to the base of the neural spine on the lateral surface of the centrum.

Ribs and intermuscular bones are preserved in specimens ZIN 312p and ZIN 314p. They are well ossified and numerous. Postmortem distortions prevent separation of the ribs and intermusculars into series. Some intermusculars are clearly branched, whereas others are not (Figs. 4A, 5B). The length of the largest intermusculars corresponds to the length of 4 or 5 abdominal centra. Apparently, there are no supraneurals.

The dorsal fin has a long and, evidently, continuous base. The dorsal pterygiophores and rays start immediately posterior to the head (ZIN 312p and ZIN 314p), and extend continuously to the end of the specimen ZIN 314p (Fig. 4A). The dorsal rays are long, segmented, and unbranched. The height of the longest dorsal rays corresponds to the length of 4 vertebrae. The lateral halves of a ray are loosely attached to each other (Fig. 5B). The dorsal fin is supported by proximal, medial and distal pterygiophores. The proximal pterygiophore is straight, rhabdoid, tapered proximally, and with a triangular distal expansion. The medial pterygiophore is shorter, rhabdoid, and constricted in the middle. The distal pterygiophore is a small round ossification at the ray base (Fig. 5B).

The pectoral fin is comparatively small, short, and narrow (Fig. 4). It is placed immediately posterior to the head and, apparently, close to the ventral edge of the body. There are about 13 segmented and unbranched pectoral rays. Among bones of the pectoral girdle, fragments of cleithrum, scapula, and also 3 radials are discernible in ZIN 314p (Fig. 4B). The scapular foramen is elliptical and enclosed in the scapula. The remains of the pectoral girdle of ZIN 310p (part of the cleithrum connected with the scapula), and one pectoral ray occupy the same position—posterior and ventral to the head (Fig. 3E).

There are no traces of pelvic fins in any of the specimens examined. Scales are also absent. Specimen ZIN 314p possesses 4 elongated sub-rectangular ossifications around the rostrum, with a shallow groove on their surface (Fig. 4B). These are, apparently, body lateral-line elements, because of their similarity with those of the Recent *Anotopterus* in shape and size.

Remarks.—The specimens from the Cenozoic of Sakhalin described above undoubtedly belong to the family Polymerichthyidae and to the genus *Polymerichthys*, because they possess huge, saber-like, inclined anteriorly palatine teeth and a continuous dorsal fin. The combination of these two characters, as far as known, is seen only in *Polymerichthys* among Teleostei. Although three of five studied specimens have no preserved elements of a dorsal fin, they share all other available characters with those with dorsal fin preserved.

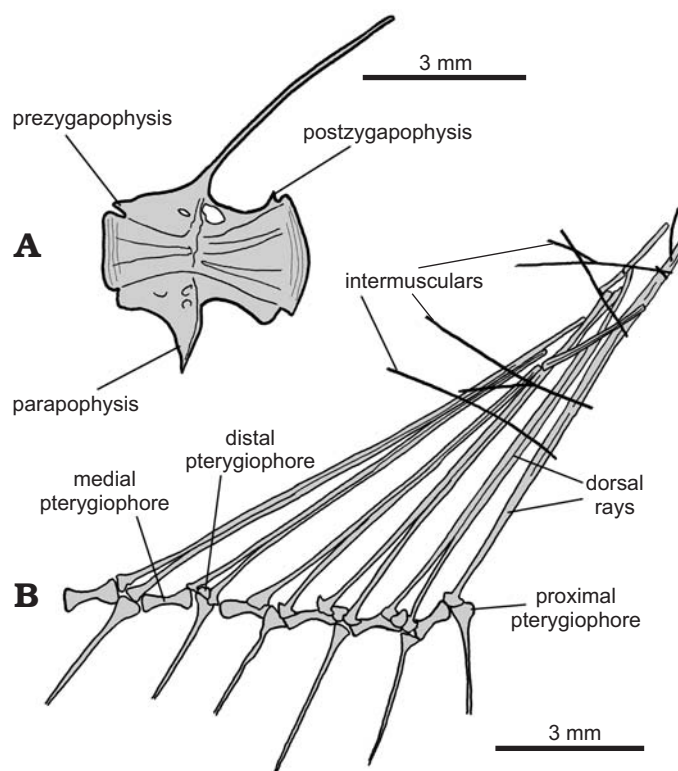


Fig. 5. Alepisauroid fish *Polymerichthys* sp. from Sakhalin Island, Holmsk Formation, late Oligocene (A) and Kurasi Formation, Middle–Late Miocene (B). A. ZIN 310p, abdominal centrum. B. ZIN 314p, fragment of the dorsal fin.

The comparison of material from Sakhalin with the description of *P. nagurai* (Uyeno, 1967) did not reveal any substantial differences. The structures of the head, of separate bones and of abdominal vertebrae, as well as the features of the dentition in *P. nagurai* are identical to those in the Sakhalin specimens. Most of the characters diagnostic for this genus and family (Uyeno 1967) are observable in fossils from Sakhalin, and are the same as in *P. nagurai*, with exception of the structure of the preorbital region, which is significantly shorter in the type specimen.

Reexamination of the holotype reveals that the anterior part of its head before the “vomeric” knob was lost when the matrix was broken off. This is visible also on illustrations in the description (Uyeno 1967: 385, fig. 1, pl. 2). Thus, the anterior part of the head of *P. nagurai*, apparently, was arranged similarly to that of the fossils from Sakhalin, i.e., with a long, prominent rostrum. Therefore, the restoration of *P. nagurai* (Uyeno 1967: 388, fig. 3) is incorrect in that the lower jaw was assumed to extend anterior to the snout. In fact, the lower jaw was probably much shorter than the prolonged rostrum.

As in the Sakhalin specimens, the holotype of *P. nagurai* possesses a ventral “vomeric” knob of the neurocranium, forked intermusculars, and the same shape and sculpture of vertebrae. *Polymerichthys* sp. from Sakhalin differs from *P. nagurai* by a greater number of teeth on the palatines: 5–7 vs. 4. Uyeno (1967) had calculated on the holotype

three large immovable palatine teeth and nine “depressible” teeth scattered around the ventral margin of neurocranium. Actually, there are four immovable, functional teeth, with the posterior one four times smaller, and eight replacement teeth with unossified bases (Uyeno 1967: 385, fig. 1). There are several comparatively large teeth around the premaxilla of holotype of *P. nagurai*, depicted in the description (Uyeno 1967: 385, fig. 1). These teeth are comparatively longer than the premaxillary teeth of specimens from Sakhalin. Because these teeth have their tips oriented dorsally, whereas the teeth from the premaxilla should be oriented mostly ventrally, they are, apparently, not premaxillary, but lower jaw teeth, displaced after fish death.

Specimen ZIN 310p differs from other specimens from Sakhalin by its very long lower jaw, which almost reaches the tip of the snout. It is also characterized by more long and slender palatal teeth and more prominent teeth on premaxillae (Fig. 3E, Table 1). Perhaps it represents another species of *Polymerichthys*. However, it is more likely that these distinctions have other explanations, for example, age variability or, more probably, sexual dimorphism. The question of the taxonomic status of ZIN 310p remains open until discovery of more representative material of fishes of this family.

In general, the specimens from Sakhalin have no essential differences from *P. nagurai*, and, perhaps, belong to the same species. Because it is impossible to exclude the possibility that several species of *Polymerichthys* existed, the paucity of available specimens precludes their identification as *P. nagurai* with confidence.

The lacking of the caudal body parts in all specimens from Sakhalin makes impossible the comparison of the caudal and anal fins structure and total number of vertebrae of these fishes with those in *P. naguriae*. Therefore, these specimens are described herein in the open nomenclature. The palatine of *Polymerichthys* sp., described from the Middle Miocene of Italy (Carnevale 2007), definitely belongs to a taxon distinct from the Pacific polymerichthyids. It differs by the greater number of palatine teeth (9 on one bone vs. 4–7 on both left and right bones) and by serrated (vs. smooth) tooth cutting edges (Carnevale 2007).

Discussion and conclusions

Morphological features of Polymerichthyidae.—The data obtained from specimens from Sakhalin, together with those from reexamination of the holotype of *P. nagurai*, add some important information on the morphology of Polymerichthyidae. The first concerns the structure of the snout of these fishes. *Polymerichthys* is unique among Aulopiformes in the presence of long rostrum formed mainly by the frontals, below which the lower jaw is included. The upper jaw symphysis and the vomer, apparently, are located far posterior to the tip of snout. Details of the snout structure can be understood only after obtaining new, better preserved materials of these fishes. The thin bony outgrowths

at the anterior ends of the rostrum and of the lower jaw of the Sakhalin specimens suggest the presence of skin projections from the tips of both jaws, similar to those on the mandible of Recent *Anotopterus* spp.

A slender and very elongated, eel-like body with a great number of vertebrae is also a main feature of Polymerichthyidae. As indicated by Uyeno (1967), there are about 186 vertebrae in *P. nagurai*. Of them, 15 vertebrae are thought to have been lost in a gap in the anterior part of the skeleton (Uyeno 1967: pl. 1). Reexamination of the holotype reveals 70 abdominal and approximately 94–97 caudal vertebrae discernible on the specimen. The exact number of posterior caudal vertebrae could not be accurately determined. If, according to Uyeno (1967), 15 abdominal vertebrae were lost in the gap, there must have been $85 + 94 - 97 = 179 - 182$ vertebrae in *P. nagurai*. The specimens from Sakhalin agree with this character by their great number of abdominal vertebrae (63 at least). The number of vertebrae in Polymerichthyidae greatly exceeds the maximal value known for aulopiforms—up to 121 vertebrae in *Stemonosudis intermedia* (Ege, 1933) of the Paralepididae (Ditty 2005).

Apparently, there were no spinules at the beginning of the anal fin of *Polymerichthys*. The anal fin rays have not been preserved in the specimens from Sakhalin. In the holotype of *P. nagurai*, the structure of the anal fin rays is similar to those of the dorsal fin. Several anterior anal fin rays lack their distal parts due to preservation, but their basal parts, consisting of two halves of the ray, are preserved and look misleadingly like spinules.

Forked intermusculars are found in the specimens from Sakhalin and also in the holotype of *P. nagurai*. In the latter, they are placed below the vertebrate column and, thus, are epipleurals. These bones are forked proximally and are attached to the parapophysis with the longest branch of a fork. This can be seen at the middle of the abdominal part of the column, below assumed vertebrae 40–60 (Uyeno 1967: fig. 2A). Both dorsal and ventral intermusculars are continuing into the caudal body region in *P. nagurai*.

Polymerichthyidae are characterized by tripartite pterygiophores at least in the dorsal fin. The pterygiophores of vertical fins are not seen in the holotype of *P. nagurai* owing to features of its preservation.

Apparently, polymerichthyids were scaleless fishes, with exception of lateral line scales, which resemble those of Recent *Anotopterus* in their shape. All specimens examined lack pelvic fins, but the quality of preservation of these specimens does not allow the presence or absence of this fin to be known with certainty. An adipose fin is, apparently, absent (Uyeno 1967).

Relationships of Polymerichthyidae.—Uyeno (1967) attributed Polymerichthyidae to the suborder Alepisauroidei, and pointed out the similarity of this extinct family with the Recent alepisauroid monotypic families Anotopteridae and Alepisauridae in elongated body and large teeth. *Polymerichthys* also resembles *Alepisaurus* in having a long-

based dorsal fin, a unique character among Aulopiformes. On the other hand, *Polymerichthys* is similar to *Anotopterus* in its enormous, saber-like and anteriorly inclined palatal teeth, a character shared only by these two genera.

Both mentioned Recent genera were traditionally included in the superfamily Alepisauroidea as separate monotypic families (Gosline et al. 1966; Rosen 1973; Johnson 1982; Johnson 1992). Baldwin and Johnson (1996), in their morphological analysis of aulopiform phylogeny, showed a close relationships between *Anotopterus* and Paralepididae, and included it in that family, whereas *Alepisaurus* was joined with *Omosudis* under Alepisauridae; both families were within the suborder Alepisauroidei.

Further phylogenetic research on Aulopiformes, based on both morphological and molecular characters, confirmed the monophyly of the clade *Alepisaurus* + *Omosudis* (Sato and Nakabo 2002; Davis 2010). Sato and Nakabo (2002) did not include the *Anotopterus* in their analysis. Davis (2010) proposed a new composition for the monophyletic family Alepisauridae consisting of *Anotopterus* + *Magnisudis* sister to *Alepisaurus* + *Omosudis*.

Among 139 morphological characters, used in the analysis of Davis (2010: 462–469, appendices 1 and 2), the condition of 26 (about 19%) can be recognized for *Polymerichthys*. Of them, 14 characters demonstrate a presumable primitive condition: quadrate fan-shaped (character 42); no concavity in dorsal margin of quadrate (44); metapterygoid overlies quadrate (46); ectopterygoid without teeth (48); hyomandibula oriented vertically or subvertically, opercle posterior to suspensorium (50); no premaxillary fenestra (56); outer tooth patch on tip of lower jaw absent (63); frontal not expanded laterally (66); most or all epipleurals attached to axial skeleton (74); long series of epipleurals (75); no fusion of pterygiophores of dorsal or anal fin (100); pterygiophores of dorsal fin not triangular proximally (101); pterygiophores of anal fin not triangular proximally (102); eyes laterally directed (128).

The following 12 characters possess the more or less derived condition: gill rakers present as toothplates (5-1); palatine is the dominant tooth-bearing bone (41-2); entopterygoid teeth absent (49-1); snout length greater than 50% head length (55-1); maxilla intact but slender, posterior end not expanded (62-1); epipleurals from about V12–V15 to near end of series forked proximally (78-1); no supraneurals (83-3); 40–60% caudal vertebrae (84-1); all neural arches closed dorsally (87-2); pectoral fins set low on body (111-1); body scales absent, lateral-line scales or structures at least partially ossified (123-1); adipose fin absent (130-1).

This character set for Polymerichthyidae is too incomplete for adequate estimation of their taxonomic position. The character of entopterygoid teeth absence (49-1) supports the clade of Alepisauroidei (Davis 2010: 458, 469, fig. 8, appendix 3). The characters of gill raker structure (5-1), palatine dentition (41-2), and pectoral fin position (111-1) support the inclusion of Polymerichthyidae in the clade of Alepisauroidea. The squamation features of

Polymerichthyidae (123-1) exclude the Scopelarchidae from its nearest relatives, and pull it together with members of clade X. The characters of relative snout length (55-1) and of abdominal/caudal vertebrae ratio (84-1) suggest inclusion of Polymerichthyidae in clade AA (Davis 2010: 458, fig. 8) consisting of Sudidae, Alepisauridae, and Paralepididae. The position of polymerichthyids within this clade cannot be defined more precisely on the data available now. However, some characters give hints to its closer relations with Alepisauridae: the structure of the maxilla (62-1) pulls together Polymerichthyidae with *Anotopterus*, whereas the absence of supraneurals (83-3), with *Alepisaurus*.

Thus, polymerichthyids are unusual extinct alepisauroids that were, obviously, very specialized deep-sea predators, widely distributed in the basins of the north-western Pacific and, probably, of Tethys at the end of the Paleogene and in the Neogene. Their taxonomic status is still unresolved, and their nearest relatives are, probably, among alepisaurids. The new findings from Sakhalin expand the known geographical distribution of Pacific polymerichthyids by more than 1500 km (or about 12° of latitude) to the north, and extend the time interval for this family to as early as the late Oligocene.

Acknowledgments

I thank Maxim S. Kartashov (Holmsk, Russia), Vladimir V. Platonov (ZIN), Igor L. Tumanov (Saint-Petersburg, Russia), and Ludmila K. Fedorova (Uzhno-Sakhalinsk, Russia) for their help in organization and carrying out of the field researches. I am grateful to Makoto Manabe, Shinya Miyata, and Gento Shinohara (all NSMT) for their kind help with collections. Many thanks to Teruya Uyeno (NSMT) and Youshitaka Yabumoto (Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan) for fruitful discussions and valuable comments. Alexei Pinchuk (University of Alaska, Fairbanks, USA) kindly agreed to improve English. Mark V.H. Wilson (University of Alberta, Edmonton, Canada) and anonymous reviewer are thanked for their constructive comments on the manuscript. I thank also Mark V.H. Wilson for extensive English corrections. Russian Foundation for Basic Research grant 14-04-00642-a supported this study.

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