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The structure of the Miocene northwestern Pacific ichthyofauna as revealed by two fossil fish assemblages from Sakhalin Island, Russia

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Abstract. Two coeval assemblages of fossil fishes came from the middle–late Miocene deposits of Sakhalin Island, Russia. The fish community from the Agnevo Formation consists of 28 species belonging to 15 families of shallow-water fishes, with the predominance of cottoids, stichaeoids, and pleuronectoids. The assemblage from the Kurasi Formation contains fossils of 35 species from 27 fish families and comprises mainly mesopelagic dwellers, such as myctophids, argentiniforms, stomiiforms, and aulopiforms. These assemblages differ mainly in the number of species belonging to extinct genera. Among the 28 fish genera known from the Agnevo Formation, 14 (50%) genera are extinct. In contrast, out of 35 genera described from the Kurasi Formation only three (about 8.6%) genera are extinct. The morphological distances between the fossil and recent congeneric species are more pronounced and defined in the shallow-water community than in the deep-water assemblage. The differences in taxonomic composition between the fossil assemblages likely reflect the different influence of the climatic and geographic events in the Neogene and Quaternary on the evolutionary rates of shallow- and deep-water fish communities.

Keywords: evolutionary rates, fishes, fossil assemblages, ichthyofauna development, Neogene

Introduction

Studies of animal fossils are fundamental for understanding the origin of the modern fauna and for hypothesizing evolutionary pathways within faunistic groups and communities. Analysis of sequential fossil groups from a location where they had been gradually replacing each other over time allows reconstruction of patterns and rates of the community evolution. Comparison of fossil and modern communities from the same biotope may reveal developmental vectors and evolutionary rates within the time interval, even though the fossil record may have substantial gaps. In this paper, I analyzed and compared two coeval fossil assemblages of mid-water and shallow-water marine ichthyofauna, which have been recovered from Neogene deposits on Sakhalin Island (Russia). Changes in the structure of these communities over prehistorical time highlight some previously unknown aspects of their evolutionary pathways.

These assemblages were found in the sediments of the Agnevo (AF) and the Kurasi (KF) formations (Figure 1). They are among the most taxonomically diverse discoveries known from Eastern Russia. Ancient fish commu-

nities, which inhabited the waters near Sakhalin Island in the Neogene, have been recently investigated. Based on extensive collections obtained during multi-year studies, the taxonomic composition of each assemblage was verified, and the morphological relationships among the taxa were examined. The fossils were collected in the coastal cliffs of the Tartar Strait on western Sakhalin at localities approximately 300 km apart (Figure 1). The AF fish assemblage represented a comparatively shallow-water fish community, which inhabited the shelf at less than 30–50 m depths (Nazarkin, 2000). Numerous well-preserved fossilized plant leaves suggest considerable runoff from the neighboring land. In addition to fishes, the fossiliferous beds contain remains of bivalves and gastropods, arthropods (Anomura, Natantia, Gammaridea), echinoderms (Echinoidea, Asteroidea, Ophiuroidea), polychaetes, bryozoans, pieces of wood and imprints of seaweed. Numerous foraminifers have been also found there (Fotyaynova and Serova, 1987).

In contrast, the KF deposits contain remains of more deep-sea organisms. The findings of crustaceans are extremely rare there. The bivalves occur more often, but in considerably lower numbers than in the AF. Occasion-

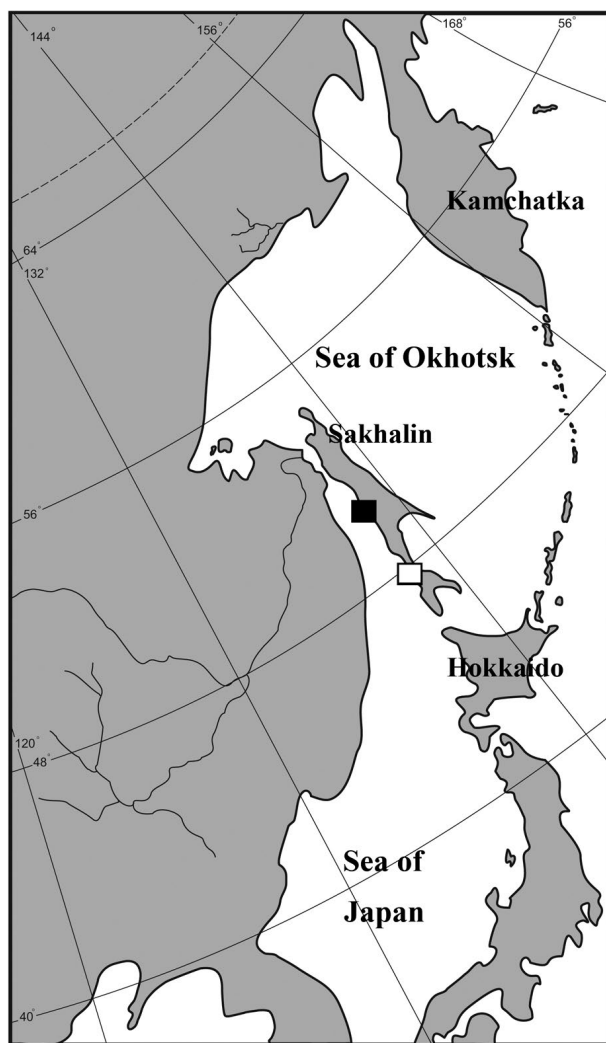


Figure 1. Sketch map showing the localities of Kurasi (open square) and Agnevo (solid square) formations.

ally vertebrae and fragments of other bones of cetaceans occur. The remains of vegetation are represented only by very small pieces of wood. At some KF localities, foraminifers and diatoms are found. The composition of the fauna of mollusks and foraminifers suggests that the accumulation depth of the deposition was significantly more than 200 m (Gladenkov *et al.*, 2002).

The fossiliferous beds of both formations were deposited approximately at the same time in the middle–late Miocene. The analysis of the structure and composition of fossil fishes of these localities and the comparison between the two fish assemblages and with the recent ichthyofauna of the Sakhalin region reveals important features of the evolution of coastal and deep-water fish fauna in the northwest Pacific during the Neogene.

Materials, methods and geological background

The fossils were collected in 1993–1998 and 2013 at the locality of the Agnevo Formation, and in 1998, 2005, 2011–2016 at the locality of the Kurasi Formation. The specimens were prepared and studied by common methods of paleontological research. About 800 specimens from each formation were collected. They include complete skeletons, skeletal fragments, and single bones. Most of the remains were identified to the species and/or genus level. The materials are deposited in the paleontological section of the fish collection of the Zoological Institute of the Russian Academy of Sciences (ZIN), St. Petersburg, Russia.

The Agnevo Formation, aka “layers of the Markevich Cape”, are distributed locally to the north and the south from the mouth of the Agnevo River. It consists of tuffs, tuff breccia, siltstones, and sandstones with a few coal layers (Kuzina and Ratnovsky, 1970). Based on the analysis of fossil flora as well as foraminifera and mollusk assemblages, the age of the AF has been determined as the middle–late Miocene within the Serravallian–Tortonian and correlated with the foraminiferal zones N13–N16 (Fotyaynova and Serova, 1987; Zubakov, 1990; Serova and Fotyaynova, 1991). The accumulation time of deposits of the AF coincides with the second large climatic optimum of the Neogene in the Russian Far East, which took place around the middle and late Miocene boundary (Fotyaynova and Serova, 1987; Gladenkov, 2004). The AF sampling locality is situated in the northern half of Sakhalin approximately 1 km to the north from the mouth of the Agnevo River (Figure 1).

The Kurasi Formation extends over both east and west coasts of southern Sakhalin. It consists of clayish aleurolites and siliceous soapstones with layers of sandstones and diatomites. These beds are known as the deepest oceanic Tertiary deposits of the Sakhalin. The deposition of the KF also had occurred during the second Miocene climatic optimum that resulted in the greatest extent of the sea in the Pacific northwest. Both the KF and the AF are of the same age typically defined as Serravallian–Tortonian (Savitskiy, 1982; Gladenkov *et al.*, 2002; Gladenkov, 2008). The richest fossil deposits of the KF are found in the coastal cliffs of the Tartar Strait 5 km south from Penzenskoye in the Tomari City district (Figure 1).

Results

Currently, a total of 28 species belonging to 28 genera, 15 families and 7 orders are known from the Agnevo Formation (Table 1). Only one family, Trispinacidae, is extinct. Trispinacidae is a group of unclear taxonomic status provisionally placed among trachinoids (Nazarkin,

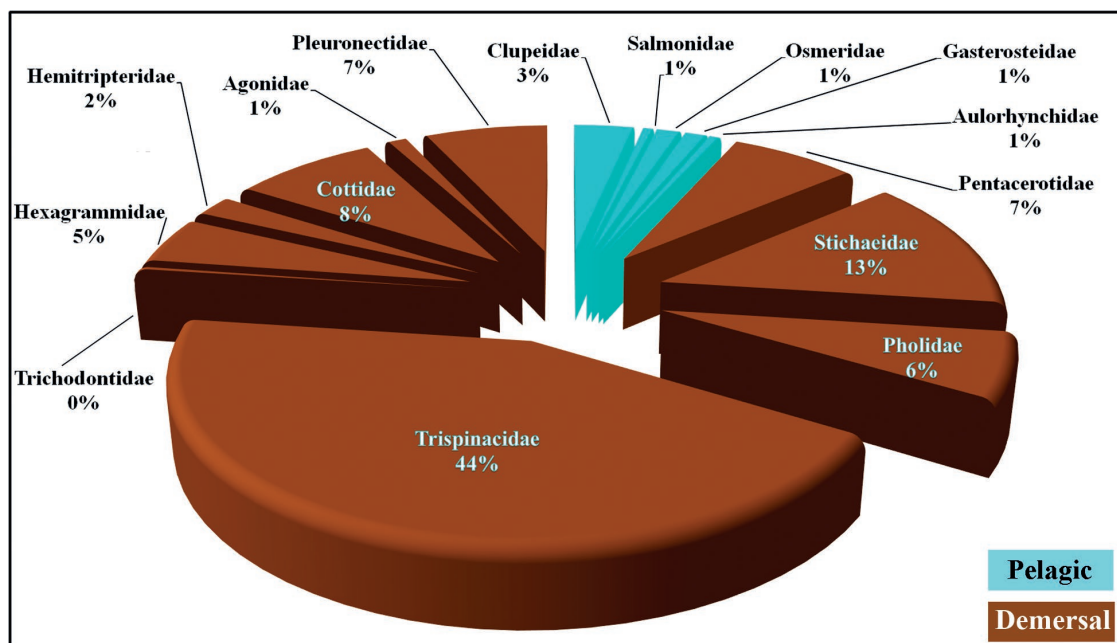
Table 1. Composition of the shallow-water fossil fish assemblage from the middle–late Miocene Agnevo Formation of Sakhalin Island: 7 orders, 15 families, 28 genera, 28 species. 14 genera are extinct. † - extinct genus or family. The genera in quotes are awaiting (re)description.

Habitat	Order	Family	Genus	species	
Epipelagic	Clupeiformes	Clupeidae	† <i>Xyne</i>	cf. <i>grex</i> Jordan et Gilbert, 1919	
	Salmoniformes	Salmonidae	<i>Parahucho</i>	sp.	
Neritopelagic	Osmeriformes	Osmeridae	†Gen.	sp.	
	Gasterosteiformes	Gasterosteidae	<i>Gasterosteus</i>	<i>abnormis</i> Gretchina, 1981	
Benthopelagic		Aulorhynchidae	<i>Aulichthys</i>	<i>miocaenicus</i> Nazarkin, 2019	
	Pentacerotidae	†“ <i>Pentaceros</i> ”		<i>sakhalinicus</i> (Gretchina, 1975)	
		†“ <i>Ernogrammus</i> ”		<i>litoralis</i> (Gretchina, 1980)	
		<i>Stichaeopsis</i>		<i>sakhalinensis</i> Nazarkin, 1998	
	Stichaeidae	<i>Stichaeus</i>		<i>brachigrammus</i> Nazarkin, 1998	
		†“ <i>Ascoldia</i> ”		<i>agnevica</i> (Gretchina, 1980)	
	Perciformes	† <i>Nivchia</i>		<i>makushokii</i> Nazarkin, 1998	
		Pholidae	† <i>Agnevichthys</i>		<i>gretchinae</i> Nazarkin, 2002
			† <i>Paleopholis</i>		<i>laevis</i> Nazarkin, 2002
	†Trispinacidae	† <i>Trispinax</i>		<i>ladae</i> Nazarkin, 2002	
	Demersal	Trichodontidae	† <i>Diaphanthes</i>		<i>tilesii</i> Nazarkin et Voskoboinkova, 2000
			† <i>Paraophiodon</i>		<i>nessovii</i> Nazarkin, 1997
		Hexagrammidae			<i>multispinata</i> Nazarkin, Carnevale et Bannikov, 2013
			† <i>Sakhalinia</i>		
Scorpaeniformes		Artediellidae	<i>Artediellichthys</i>		<i>candelabrum</i> Nazarkin, 2019
			<i>Artediellus</i>		<i>simplex</i> Nazarkin, 2019
			Cottidae	<i>Enophrhys</i>	
			<i>Icelus</i>		sp.
			Gen. indet.		sp.
		Hemitripteridae	† <i>Hemitripterella</i>		<i>granulata</i> Nazarkin, 1999
Pleuronectiformes	Agonidae	<i>Bothragonus</i>		sp.	
		<i>Clidoderma</i>		sp.	
	Pleuronectidae	<i>Hippoglossus</i>		sp.	
		† <i>Psettoraptor</i>		<i>armatus</i> Nazarkin, 2002	
		<i>Limanda</i>		<i>asperoides</i> (Nazarkin, 1997)	

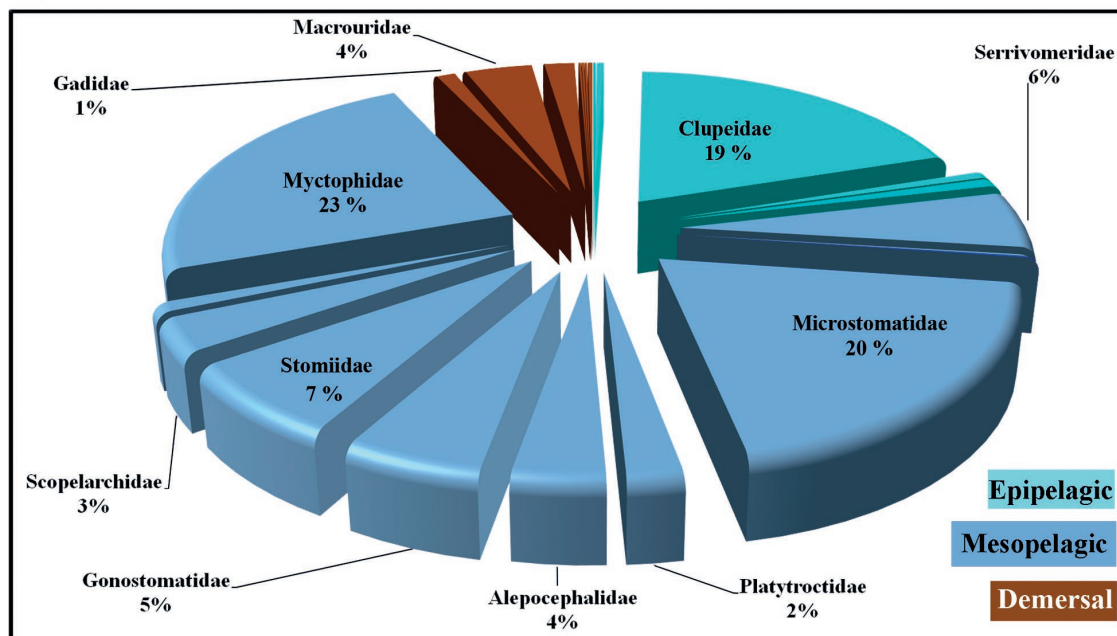
2002). Trispinacidae remains are known only from the AF. The only species of this family, *Trispinax lada* Nazarkin, 2002, dominates the AF community accounting for about

44% of all fish remains.

The other Miocene fishes from the AF are representatives of Recent families. In the modern fauna, the



A



B

Figure 2. Structure and composition of the fossil fish assemblages from the Agnevo Formation (A) and from the Kurasi Formation (B). The relative abundance of the remains is expressed in %.

members of these families are bottom or near-bottom dwellers in littoral or sublittoral zones of the shelf to the depth of the continental slope, i.e., about 200 m, and rarely deeper. Except for trispinacids, all demersal fishes in the AF comprise 50% of all collected remains. The greatest taxonomic diversity came from the suborders Sticheoidei,

Cottoidei, Pleuronectoidei, and the families pricklebacks Stichaeidae, sculpins Cottidae and flatfishes Pleuronectidae (Table 1, Figure 2A). In the modern fauna, only benthopelagic armorheads (*Pentaceros*) and some flatfishes (*Hippoglossus*, *Clidoderma*) can inhabit the depth below 1000 m (Fedorov *et al.*, 2003). Only four species belong

Table 2. Composition of the deep-water fossil fish assemblage from the middle-late Miocene Kurasi Formation of Sakhalin Island: 14 orders, 27 families, 35 genera, 35 species. Three genera are extinct. † - extinct genus or family.

Habitat	Order	Family	Genus	Species
Epipelagic	Lamniformes	Lamnidae	<i>Isurus</i>	<i>planus</i> (Agassiz, 1856)
		Cetorhinidae	<i>Cetorhinus</i>	cf. <i>maximus</i> (Gunnerus, 1765)
Mesopelagic	Anguilliformes	Serrivomeridae	<i>Serrivomer</i>	sp.
		Nemichthyidae	<i>Avocettina</i>	sp.
Epipelagic	Clupeiformes	Clupeidae	† <i>Eosardinella</i>	<i>hishinaensis</i> Sato, 1966
		Opisthoproctidae	<i>Macropinna</i>	sp.
Mesopelagic	Argentiniiformes		Bathylaginae gen. indet.	sp.
		Microstomatidae	<i>Leuroglossus</i>	<i>kobylianskyi</i> Nazarkin, 2018
			cf. <i>Pseudobathylagus</i>	sp.
	Alepocephaliformes	Platyroctidae	<i>Holtbyrnia</i>	sp.
		Alepocephalidae	<i>Bajacalifornia</i>	sp.
			<i>Leptochilichthys</i>	cf. <i>agassizii</i> Garman, 1899
Mesopelagic	Stomiiformes	Gonostomatidae	<i>Cyclothone</i>	<i>mukhachevae</i> Nazarkin, 2015
		Phosichthyidae	<i>Vinciguerria</i>	sp.
		Stomiidae	<i>Chauliodus</i>	<i>testa</i> Nazarkin, 2014
	<i>Melanostomias</i>		sp.	
	Aulopiformes	Scopelarchidae	<i>Benthalbella</i>	<i>praecessor</i> Nazarkin et Carnevale, 2018
			Gen. indet.	sp.
†Polymerichthyidae		† <i>Polymerichthys</i>	cf. <i>nagurai</i> Uyeno, 1967	
Myctophiformes	Myctophidae		†Gen.	sp.
		<i>Diaphus</i>	sp.	
		<i>Lampanyctus</i>	sp.	
Demersal	Gardiformes	Gardidae	Gen. indet.	sp.
		Macrouridae	<i>Coryphenoides</i>	sp.
			Gen. indet.	sp.
Mesopelagic	Bericiformes	Melamphidae	<i>Scopelogadus</i>	sp.
Epipelagic	Gasterosteiformes	Gasterosteidae	<i>Gasterosteus</i>	cf. <i>aculeatus</i> Linnaeus, 1758
	Perciformes	Scombridae	<i>Scomber</i>	sp.
		Anarhichadidae	Gen. indet.	sp.
		Stichaeidae	Gen.	sp.
Demersal	Scorpaeniformes	Setarchidae	<i>Setarches</i>	sp.
		Sebastidae	<i>Sebastes</i>	sp.
		Cottidae	<i>Myoxocephalus</i>	sp.
	Pleuronectiformes	Hemitripteridae	<i>Nautichthys</i>	sp.
		Pleuronectidae	Gen. indet.	sp.

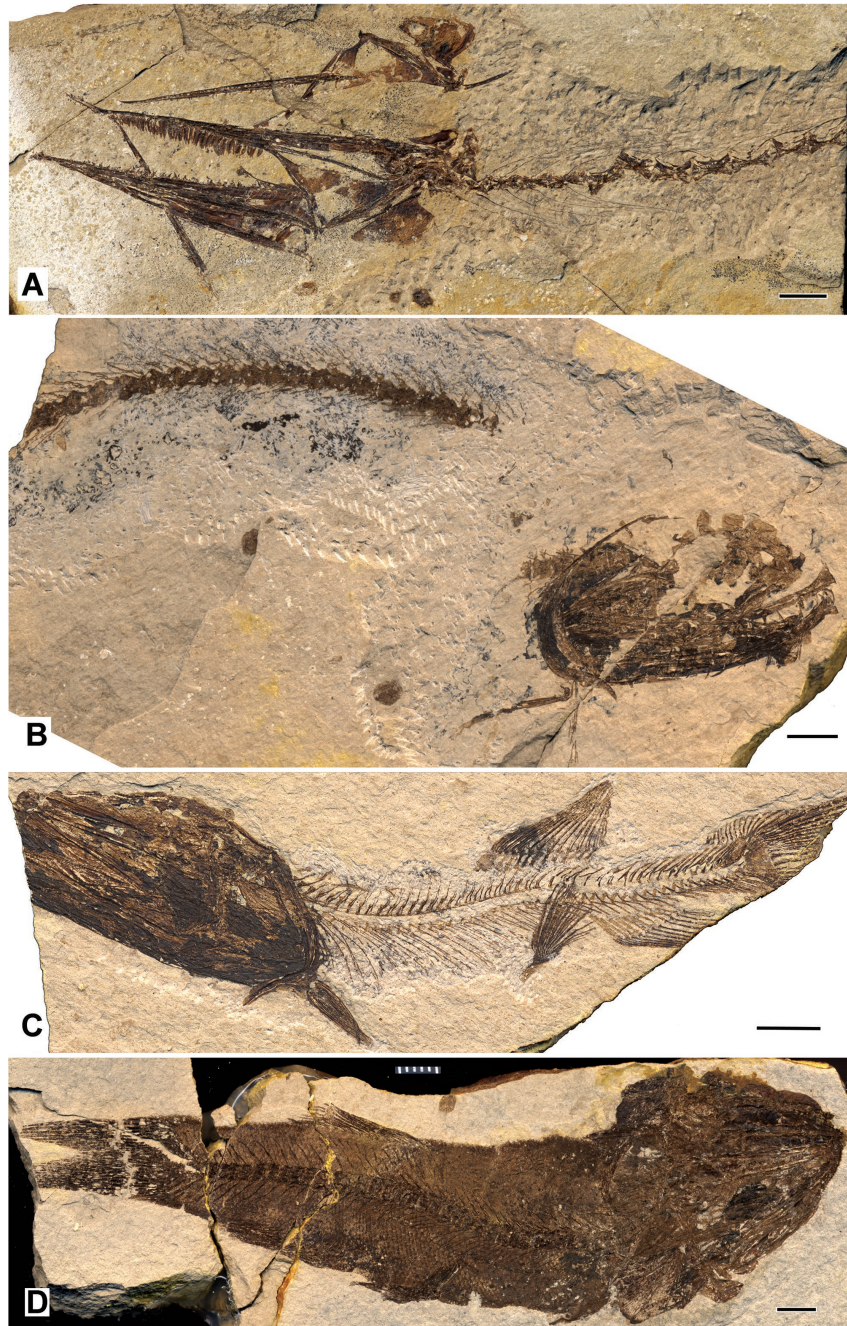


Figure 3. Some representatives of the mid-water fish association of the Kurasi Formation from ZIN collection: sawtooth eel *Serrivomer* sp., ZIN 464p (A); dragonfish *Melanostomias* sp., ZIN 462p (B); slickhead *Leptochilichthys* sp., ZIN 446p (C); tubeshoulder *Holtbyrnia* sp., ZIN 463p (D). Scale bars equal 5 mm.

to the group of nerito-pelagic fishes—herrings, salmons, smelts, and sticklebacks, whose cumulative part in this community is little more than 6% of collected skeletons.

The assemblage from the Kurasi Formation contains the remains of 35 species from 35 genera, 27 families of 14 orders (Table 2). Over 71% (Figure 2B) of the fossils

belong to the pelagic deep-water fauna which is dominated by three forms of lanternfishes (Myctophidae) at least, and followed by deep water smelts (Microstomidae, primarily *Leuroglossus*). The other common taxa include viperfishes (*Chauliodus*), dragonfishes (*Melanostomias*), bristlemouths (*Cyclothone*), sawtooth eels

(*Serrivomer*), pearleyes (*Benthalbella*), slickheads (*Bajacalifornia*) and tubeshoulders (*Holtbyrnia*) (Figure 3). The findings of the snipe-eels Nemichthyidae, barrelyeys *Macropinna* sp., lightfishes *Vinciguerria* sp., smoothheads *Leptochilichthys* sp. and pricklebacks Stichaeidae are rare. The majority of the fossils belong to currently existing families, except for now-extinct polymerfishes–Polymerichthyidae of Aulopiformes (Uyeno, 1967).

The epipelagic fishes account for about 21.4% of all collected skeletons. In this group, the remains of extinct sardine *Eosardinella hishinaiensis* Sato, 1966 predominate. The species was widely distributed in the region of Sakhalin, Japanese and Kuril Islands in the Oligocene and Miocene (Yabumoto and Uyeno, 1994; this report). In addition to sardines, the remains of sticklebacks very similar to the extant *Gasterosteus aculeatus* Linnaeus, 1758 are found. The findings of mackerels (*Scomber*) and sharks (*Isurus* and *Cetorhinus*) are very rare.

The remains of benthic fishes constitute only 7.1% of all fossils from the KF. This part of the assemblage consists of grenadiers Macrouridae, cods Gadidae, and sea perches Sebastidae and Setarchidae. The remains of flatfishes Pleuronectidae and cottoids are very rare (Table 2).

Discussion

The common feature of both Miocene fish assemblages is that they include fishes mainly from extant families. The extinct monotypic families are playing different roles in the ancient communities. Trispinacids are dominated in the AF assemblage, and several times exceed the number of fishes in any other family (Figure 2A). At the same time, polymerfish skeletons are rare in the KF assemblage accounting for <1% of total remains. Probably the Miocene fishes of extinct families were relicts of pre-Miocene fauna, although no definitive evidence yet exists.

The taxonomic composition and the dominant fish families of both Miocene assemblages are generally similar to those inhabiting the modern seas around Sakhalin and Japan. As in the AF assemblage, cottoids, zoarcoids, and pleuronectoids contribute most to the taxonomic diversity of the modern demersal fauna of Japan, Okhotsk, and Bering seas (Borets, 1997). Similar to the KF Miocene association, the lanternfishes, microstomatids, and various stomiiforms predominate in the modern deep waters (Fedorov, 1978). Therefore, the structure of the recent ichthyofauna at the family level had been generally formed by the Miocene. At the same time, the Miocene benthic fishes were significantly less diverse than the modern ones, because the remains of such species-rich families of the modern fauna as Zoarcidae and Liparidae are absent from both Miocene assemblages.

The ratio of the extant and extinct genera differs

between the AF and the KF assemblages. While the KF assemblage contains only three extinct genera from 35 (about 8.6%), the same proportion for the AF is 14 from 28 (50.0%). While extinction of genera occurred in all ecological groups of fishes, it appears to have affected mesopelagic fishes least. Apparently, the majority of modern fish genera have appeared in the northwestern Pacific during the Neogene. In contrast, the deep-water component gained the modern genera composition, in general, in the middle Miocene.

Comparative analysis of morphological differences of the Miocene species from their extant congeners reveals, as a rule, that mesopelagic fishes have lesser distance among them than demersal shallow-water dwellers. Thus, the Miocene species from the AF reliably differ from the extant relatives in the complex of characters including body proportions, counts, and, most important, in some morphological features. The following AF fishes can serve as examples.

Neogene stickleback *Gasterosteus abnormis* Gretchina, 1981 has a reduced posterior process of the pelvic girdle, while the other parts of this girdle are normally developed (not characteristic of the extant *Gasterosteus* spp.). The fish has 38 lateral plates (vs. not more than 35–36 in Recent congeners) and body size up to 112 mm SL, which is close to the maximal SL recorded in the modern sticklebacks (Sytchevskaya and Gretchina, 1981). Miocene *Stichaeus brachigrammus* Nazarkin, 1998 differs by the very short lateral line body canal, which is only slightly entering the caudal body part, whereas in the extant *Stichaeus* spp. this canal comes far from the beginning of the anal fin (Nazarkin, 1998). The topography of the lateral body canals of *Stichaeopsis sakhalinensis* Nazarkin, 1998 from the AF is species-specific and is not congruent to any extant species of this genus (Nazarkin, 1998).

Neogene sculpin *Artdiellichthys candelabrum* Nazarkin, 2019 is characterized by well-developed preopercular spines (vs. the third spine usually much reduced in the sole extant species), by the ontogenetically variable shape of the upper preopercular spine (vs. not variable), and by an arrangement of the skin bony prickles along the whole body to the caudal fin base (vs. few prickles under the pectoral fin only) (Nazarkin, 2019). The horned sculpin from the AF, *Enophrys hoplites* Nazarkin, 2017, differ from the extant species of the same genus by the larger number of anal fin rays (14 vs. 9–13), smaller head, the flat dorsal contour of the neurocranium, and the right angle between the upper preopercular spines (vs. acute angle) (Nazarkin, 2017). Miocene flatfish *Limanda asperoides* (Nazarkin, 1997) has the smallest values of counts in its genus, and ontogenetic variability of the scales structure, unknown among the extant congeners (Nazarkin, 1997, this report).

The Miocene species of mesopelagic fishes from KF are morphologically very close to the extant representatives of the same genera. Extinct deep-water fishes usually differ from the extant congeners in the modal values of the counts, some body proportions, and the shape of separate bones.

For instance, the barreleye *Macropinna* sp. from the KF differs from the only extant species *M. microstoma* Chapman, 1939 by body proportions and the smaller number of anal rays (9 or 10 vs. 11–12), and it cannot be reliably separated from the extant species by the characters available (Nazarkin, 2016). Neogene *Cyclothone mukhachevae* Nazarkin, 2015 is very similar to the recent *C. atraria* Gilbert, 1905, from which it differs only in the lower number of teeth on maxillary and the position of the beginning of the dorsal fin base shifted posteriorly from the beginning of the anal fin (vs. at the same level) (Nazarkin, 2015). The viperfish, *Chauliodus testa* Nazarkin, 2014 from the KF is very close to the extant *Ch. macouni* Bean, 1890, and differs from it in the short predorsal distance and the shorter head along with the ossified vertebral centra of the cervical region (Nazarkin, 2014). The fossil pearleye *Benthalbella praecessor* Nazarkin et Carnevale, 2018 shares all traditional diagnostic features with the extant *B. dentata* (Chapman, 1939) (Johnson, 1974). This Miocene species differs from the extant congener only in slightly higher pectoral rays number (26–28 vs. 21–24) and in the different shapes of some visceral bones (Nazarkin and Carnevale, 2018). Because the differences of most of the Miocene mesopelagic fishes from their extant congeners are usually not so striking, these Miocene forms can be treated as morphologically closest to hypothetical ancestors of the extant species.

The results of the analysis show that the taxonomic structure of coastal fish communities has undergone considerable changes at the species level and in the genera composition since the middle–late Miocene. The same can be noted also for pelagic components of both communities where the Neogene genera of the dominant family Clupeidae were replaced by the extant *Clupea*, *Sardinops*, etc. In contrast, the taxonomic structure of deep-water pelagic fishes has changed little.

The climatic and geographical events of the Neogene and Quaternary must have affected the development of the biota in the northwest Pacific. At the beginning of the middle Miocene, sea level reached the western Sakhalin through the Japan-Sea rift for the first time (Gladenkov *et al.*, 2002; Barnes, 2003). At that time, the northwestern Pacific region between Hokkaido and Kamchatka was characterized by similar climatic conditions of the mild- or cool-temperate realm (Ogasawara, 1994). Since the middle Miocene, the Sakhalin region underwent considerable changes resulting from the development

of the Japan Sea rift, shifts in coastline configurations, transgressive cycles, and temperature fluctuations. For example, from the middle Miocene to the beginning of Pleistocene before the Ice Age, there were three large warmings against the background of the progressing cold, three large sea transgressions, and three periods of the strengthened volcanic activity (Gladenkov *et al.*, 2002).

Apparently, evolutionary responses of the deep- and shallow-water fish faunas to the changing environment were not identical. The analysis of the Neogene sea fish assemblages of Sakhalin suggests that the coastal communities were affected more than the deep-water ones, as indicated by the degree of changes in their taxonomic structure to the present time. Thus, the rate of evolution of coastal fishes since the middle–late Miocene was substantially higher, than those of deep-water dwellers.

By the middle Miocene, the region where the outcrops of the KF and the AF are located was already a part of the ancient Sea of Japan basin, and it was inhabited by the deep-sea fishes. However, the modern Sea of Japan lacks primary deep-water fishes (Shinohara *et al.*, 2011). The extinction of the deep-sea dwellers in the Sea of Japan is related to the Pleistocene regressions and subsequent anoxic events in its deeper parts (Tyler, 2002). Today, the basins of the Sea of Japan and of the Pacific Ocean are linked only by narrow shallow straits, which prevent recolonization by deep-sea organisms.

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