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A remarkable new paleoniscoid fish (Osteichthyes: Actinopterygii) from the Lower Carboniferous of Tuva Republic (Russia)

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Abstract. An unusual new palaeoniscoid, *Senekichthys hirundo* gen. et sp. nov., is described from the Lower Carboniferous of the Tuva Republic (Southwestern Siberia) of Russia. In the shape of its anal and caudal fins this new taxon resembles the peculiar palaeoniscoid *Dwykia analensis* Gardiner, 1969 from the Lower Carboniferous of South Africa, but the very incomplete record of the latter gives no possibility to place both forms in a single family. In general view *Senekichthys* seems to be most similar to the family Elonichthyidae, but many derived characters occurring in the new taxon (e.g., long and pointed snout, large orbit with regard to the postorbital head length, very long and slim caudal lobe, very long and short-based anal fin, fulcral scales on the upper caudal lobe ending well before its distal tip, absence of ridge scutes, etc.) support its classification outside of the elonichthyids. Therefore *Senekichthys* is considered as a Palaeoniscimorpha *incertae sedis*. The Lower Carboniferous fish faunas of Western Siberia are briefly discussed and compared.

Key words: actinopterygians, Lower Carboniferous, new species, palaeoniscoids, Southwestern Siberia

Introduction

The present paper is devoted to the description of a very unusual palaeoniscoid fish from the Lower Carboniferous of the Tuva Republic. Although the available specimen is incompletely preserved, its finding seems to be very interesting because it provides a new datum on the diversity of the Lower Carboniferous palaeoniscoids, and, furthermore, the new form resembles morphologically the poorly known family Dwykiidae. This monotypic family was erected by Gardiner (1969) for *Dwykia analensis*, which is known only by the very incomplete holotype from the Lower Carboniferous of South Africa. Since the holotype of *D. analensis* is represented by the posterior part of the body wanting dorsal and pelvic fins, its generic similarity to the newly described form is questionable. Judging from their disjunct distribution, the Tuva and South African forms possibly belong to separate genera; however, this hypothesis cannot be confirmed formally before collecting of new materials for both these forms. Because of that, I erect a new genus for the Tuva form for the following reasons: (1) there are several differences between the fish from Tuva and *D. analensis*, indicating they belong at least to different species; (2) the Tuva form cannot be assigned to any other palaeoniscoid genus known to date, and (3) the characters supporting the erection of the family Dwykiidae are encountered also in some other phyletically distant lineages of the palaeoniscoids. As numerous important morphological features remain unknown for the newly described form, it can be classified only as Palaeoniscimorpha *incertae sedis*.

The specimen examined is deposited in the Paleontological Institute (PIN) in Moscow.

Notes on geography, stratigraphy, and paleoenvironments

The Tuva Republic is situated at the southeastern limit of Western Siberia close to the Russian-Mongolian boundary (Figure 1a). The specimen described herein is found in the ravine of Senek Creek, which belongs to the Upper Enissei drainage. The fossil site is situated 20 km southwest of Shagonar City.

The fish-bearing layers belong to the Herbesskaya Formation of the Lower Carboniferous (upper part of

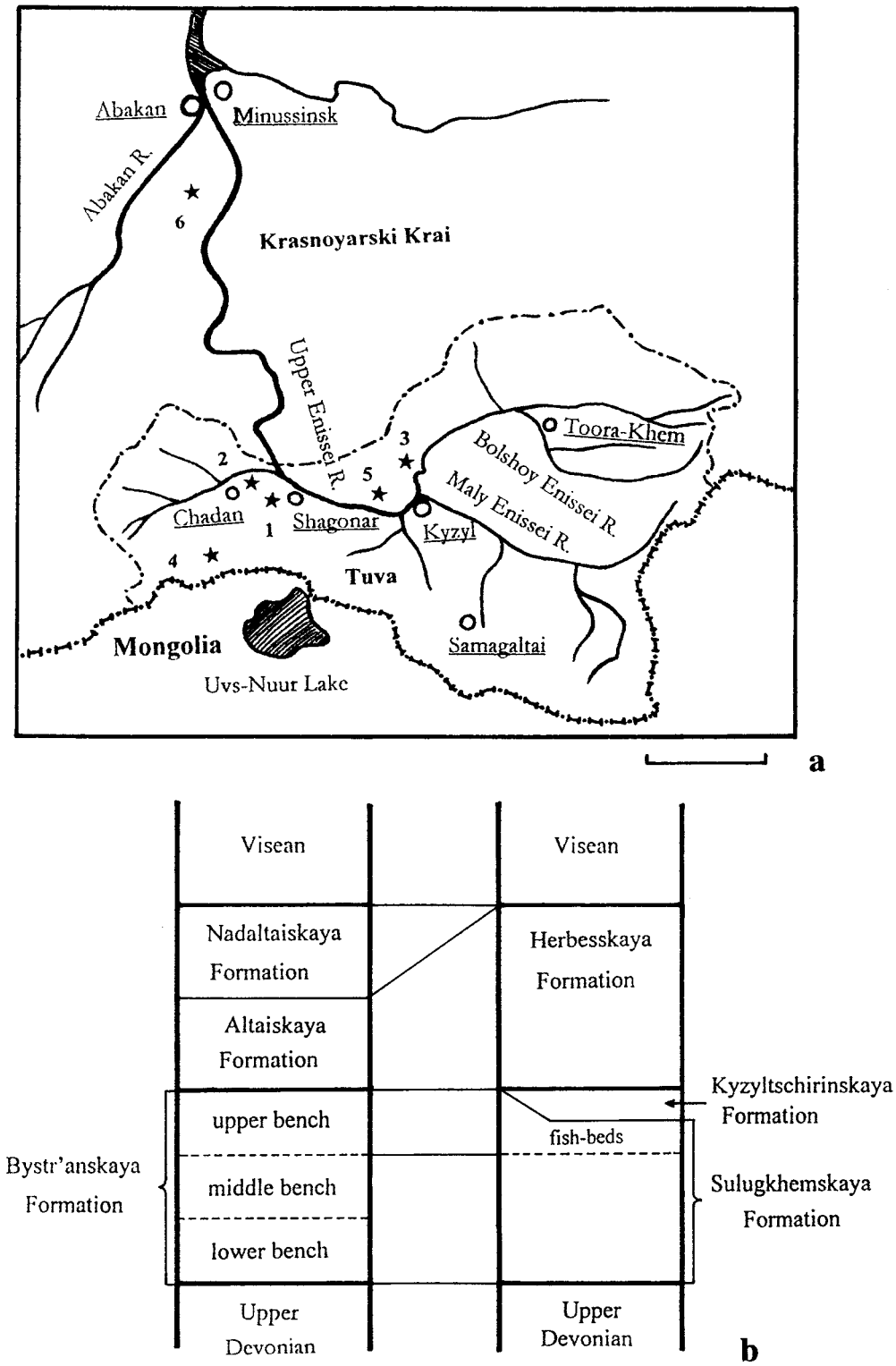

Figure 1. **a**. Map of a section of Western Siberia illustrating the locations of the fossil sites with fish remains (★): 1–3, Upper Tournaisian (Herbesskian): 1, the Senek Creek; 2, the Ortokhoden Creek; 3, the Stone Key; 4–6, – Lower Tournaisian (Sulugkhemskian (4, 5) and Bystr'anskian (6)): 4, Borschin-Gol; 5, Herbess Ridge; 6, Minussinsk Depression. Scale bar 150 km. **b**. Correlations of the regional stages of the Tournaisian of Western Siberia.

the Tournaisian Stage – Figure 1b). These rocks are composed mostly of yellowish-grey, reddish, or less often lilac-brown silicified tuffs and tuffites, and variously grained polymictic and quartzous sandstones alternating with interbeds of gritstones and limestones. So far as is known, the fossils of the Herbesskaya Formation are represented by fishes and plants. The fossil plants of the Herbesskaya Formation belong to the Upper Tournaisian Stage, but also share some similarities with Lower Visean floras (Danilevich and Vasiliev, 1966: 206). Formerly the fish remains were reported only from the Stone Key locality (Danilevich and Vasiliev, 1966), however, two other sites with fish remains are known at present: Senek Creek, and the left bank of Ortokhoden Creek (see Figure 1a). Apart from the newly described taxon the Herbesskian actinopterygian complex includes an undescribed genus and species of Amphicentridae, and undeterminable fragments of apparently more than one species of fish having a typical palaeoniscoid appearance, which apparently were cited as ''*Ganolepis* sp.'' formerly (Danilevich and Vasiliev, 1966). Moreover, *Acanthodes* sp., *Cycloptychius* sp. and *Cladodus* sp. were reported from the Herbessakaya Formation (Danilevich and Vasiliev, 1966), however, all these determinations are provisional, and no systematic revision of this fauna was made. All the known fish remains were collected in the tuffaceous rocks (Danilevich and Vasiliev, 1966; present data). The paleoenvironmental reconstructions indicate that, in conditions of the peneplained source area, there was a large but shallow subsaline landlocked sea in Herbesskian time (Danilevich and Vasiliev, 1966).

The Herbesskian fish complex is quite different from the lowermost Tournaisian fish complexes of Western Siberia. In Tuva the Lower Tournaisian consists of the Sulugkhemskaya and Kyzyltschirinskaya Formations; the latter has an incomplete cycle of sedimentation, lacks fossils, and over most of the territory is destroyed by pre-Herbesskian denudation. From the Sulugkhemskaya Formation *Strepsodus siberiacus* Chabakov, *Rhizodopsis savenkovi* Obruchev, and ''*Acanthodes* (?) *lopatini*'' are known (Danilevich and Vasiliev, 1966). All these forms are the same as in the Bystr'anskaya Formation of the Minussinsk Depression, which undoubtedly belongs to the basal Tournaisian (Graizer, 1957). There is no information about the actinopterygian remains from the Sulugkhemskaya Formation; however, this can be explained by the fact that the latter complex is known from the top of the formation only, and it correlates with the upper bench of the Bystr'anskaya Formation, where *Strepsodus* and *Rhizodopsis* are quite abundant but the palaeoniscoids have disappeared (Graizer, 1957). The palaeoniscoid complex distributed in the middle bench of the Bystr'anskaya Formation are quite different from the other Lower Carboniferous complexes of the world as most of the genera (five out of seven) belong to the endemic families Gyrolepidotidae and Palaeobergiidae (Kazantseva, 1968). This fact is not unusual because of the lacustrine origin of this fauna. On the other hand, the Herbesskian complex seems to be similar to the fish fauna of the Upper Witteberg series (South Africa, Visean) according to the presence of the new form, whose ascription to the family Dwykiidae cannot be rejected formally at present, as well as the amphicentrids. It is interesting that, according to Gardiner (1969: 424–425), the Upper Witteberg fishes inhabited a subsaline basin similar to the Tuva forms. Gardiner (1969: 450) discussed the faunistic relationships between the Tournaisian-Visean fish faunas of South Africa and Western Europe. The similarities (on the family level) between these complexes are probably caused first by the marine origin of their fish faunas, and, on the other hand, by their similar age of Late Tournaisian-Visean.

The correlations between the Western Siberian regional stages of the Tournaisian are shown in Figure 1b. The analog of the Herbesskaya Formation in the Minussinsk Depression is the Altaiskaya Formation, the rocks of which are lithologically similar, however, the latter lacks fossils (Graizer, 1957).

Systematic paleontology

Palaeoniscimorpha *incertae sedis*

Senekichthys gen. nov.

Type species.—*Senekichthys hirundo*, sp. nov.; monotypic genus.

Etymology.—From Senek Creek, and *-ichthys* (Greek), fish; masculine.

Diagnosis.—Same as that of the type species.

Senekichthys hirundo sp. nov.

Holotype.—PIN, nr. 4890-3, complete skeleton representing an imprint on matrix, with limits of the skull bones and with ornamentation of bones and scales not clearly visible; single plate without counterpart (Figure 2a); left slope of the ravine of Senek Creek, 20 km southwest of Shagonar City, Tuva Republic, Russia; Herbesskaya Formation, Lower Carboniferous (Upper Tournaisian). Species known only by the holotype.

Etymology.—Species named after *hirundo* (Latin),

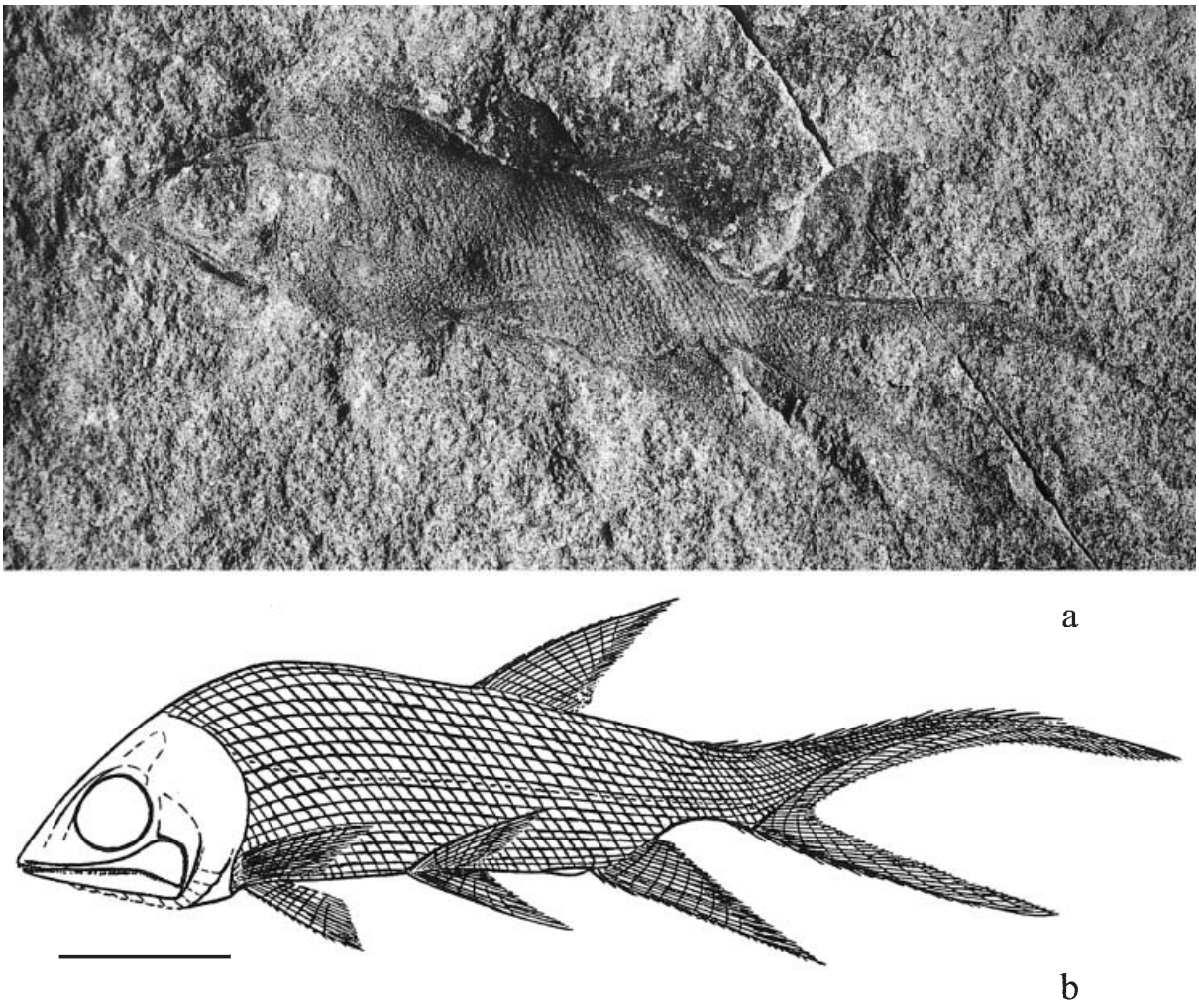

Figure 2. *Senekichthys hirundo* gen. et sp. nov., Lower Carboniferous (Tournaisian) of Tuva Republic (Russia: Southwestern Siberia). **a**. Holotype, PIN, nr. 4890-3 (natural size). **b**. Reconstruction of the lateral view. Scale bar 15 mm.

a swallow.

Diagnosis.—Fish of relatively small known size (nearly 10 cm total length). Body fusiform, but distinctly humped immediately behind the occiput (Figure 2b). Maximum body depth contained nearly 5 times in the total length (TL). Caudal peduncle rather short (approximately 12 times in TL) and low, its least depth nearly 1.5 times smaller than its length. Head moderately long, contained approximately 5 times in TL. Snout pointed, with jaws equal or nearly so. Jaw teeth conical, arranged in a single series. Orbit placed not far anteriorly, very large, round, its diameter contained nearly 2.25 times in the head length and only slightly smaller than postorbital length of head. Anterior portion of maxillary longer than its postorbital plate. Postorbital plate of maxillary moderately deep. Mandibular suspension apparently only slightly oblique. Nasal long, contacting the narrow dermosphenotic. Dorsal fin origin much closer to caudal fin base than to snout tip, but well in front of that of anal fin. Anal fin long but with very narrow insertion (on about five scale rows), with approximately 20 rays. Pelvic fins long but short-based, and inserted in front of the level of dorsal fin origin, equidistant from the pectoral fin and anal fin origins. Caudal fin heterocercal, inequilobate, and deeply clefted. Scaly lobe of the caudal fin elongated and slim; caudal inversion line progressive. Pterygial formula approximately $\frac{21}{7\ 20\ 34}4$. Fin rays very fine, articulated, and distally bifurcating. At least some of the fins with fringing fulcra. Fulcral scales on both upper and lower caudal lobes very long and narrow, needlelike, not reaching the tips

of the lobes. Flank scales small and rhomboidal. Ridge scutes absent, but a single enlarged scale occurs before the anal fin origin.

Description.—The limits and ornamentation of the skull bones including the opercular series are not clearly seen. Besides the characters given in the diagnosis there are several additional features. Both the pectoral and pelvic fin rays are long, their tips not or hardly reaching the pelvic and anal fin origin levels, respectively. The length of the longest pelvic fin rays is approximately 2.5 times greater than the length of the pelvic fin base. The length of the longest anal fin rays is 3 times greater than the length of the anal fin base, and only 1.2 times shorter than the length of the lower caudal lobe. The pelvic fin rays are approximately 15 in number. The number of the dorsal, pectoral, and caudal fin rays cannot be counted accurately. There are approximately 50–60 transverse rows of scales from cleithrum to the inclination of the scales anterior to the caudal fin base. There are approximately 17 scales (perhaps slightly more, as the limits of scales along the dorsal and ventral contours of body are not exactly visible due to the state of preservation) in an oblique row between the levels of the dorsal and anal fin origins. The middle flank scales are approximately 1.5 times deeper than long; the presence/absence of serrations on the posterior scale borders, scale ornamentation and the type of articulation are not determinable. There are approximately 15 (or slightly more) fulcral scales on the upper caudal lobe. The body lateral line is single, mediolateral.

There are several measurements of the holotype (in mm): total length 105; length from the tip of the snout to the caudal base 65; head length 18; orbital diameter 8; maximum body depth 21; least depth of caudal peduncle 5.5; length of the caudal peduncle 8; predorsal distance 43; prepelvic distance 38; preanal distance 50; pectoral fin length *ca*. 15; pelvic fin length *ca*. 15; pelvic base length *ca*. 6; length of the longest dorsal fin ray *ca*. 18; length of the longest anal fin ray 21; length of the anal fin base 7; length of the upper caudal lobe 40; length of the lower caudal lobe 25.

Discussion

Senekichthys hirundo is unique among all the palaeoniscoids known to date in possession of the following characters in combination: very long and short-based anal fin containing approximately 20 rays; very slim and long scaly caudal lobe, and caudal fin only 1.6 times shorter in length than both the trunk and head; very long but short-based paired fins; long and pointed snout without distinct rostrum; very large orbit being commensurable with postorbital head length and placed not so far anteriorly. All these characters are quite rarely met with in the palaeoniscoids, and never or only partially in the same combination. Thus, the separate taxonomic position of the Tuva form is indisputable; however, none of these characters are informative for the phylogenetic relationships of the new taxon.

Senekichthys is characterized by two features which are basic for the poorly known family Dwykiidae from the Lower Carboniferous of South Africa. This family is known by a single very incomplete specimen, the holotype of *Dwykia analensis*, which is represented by the posterior half of the body wanting dorsal and pelvic fins. *Senekichthys* agrees with Gardiner's (1969) diagnosis of Dwykiidae in possession of a very long anal fin with a very narrow insertion, which is the only diagnostic feature of this family. The elongate and slim caudal scaly lobe is another important character similar in both *Senekichthys* and *Dwykia*. According to the original figure (Gardiner, 1969, pl. 1) this specimen seems to be incompletely prepared, the posterior halves of the caudal lobes being covered with matrix, but apparently the caudal fin of *D. analensis* is similarly shaped as in *S. hirundo*. The only available differences between *D. analensis* and *S. hirundo* are the number of the anal fin rays (16 in *D. analensis* vs. 20 in *S. hirundo*), and a more delicate caudal peduncle in *S. hirundo* (its least depth nearly 1.5 times smaller than its length vs. caudal peduncle length nearly the same as its depth in *D. analensis*). All these differences are no more than specific ones, but the very incomplete preservation of *D. analensis* does not allow asserting a generical similarity between the Tuva and the South African forms.

On the other hand, an elongated and slim anal fin with a more or less narrow insertion is encountered in some other palaeoniscoids such as *Acropholis stensioei*, *Mansfieldiscus*, *Uydenichthys* and *Acrolepis ortholepis*; therefore, this character alone cannot support the monophyletic origin of *Dwykia* and *Senekichthys* (Dr. Cécile Poplin, personal communication 2003). But none of these taxa agree with *Senekichthys* in the other principal respects mentioned above. Thus, *Senekichthys* has no close relationships to any of these palaeoniscoids. The elongated and slim caudal scaly lobe also occurred in some paleoniscoids (e.g., *Korutichthys*, *Uydenia*, *Gardineria*, *Pteroniscus*, *Pygopterus*, etc.), but in other respects these genera also sharply differ and, as a result, have no close relationships with *Senekichthys*.

In general appearance *Senekichthys* looks like the family Elonichthyidae in the following combination

of characters: anterior portion of the maxillary longer than its postorbital part, the deeply cleft caudal fin, the similar body form, fins position, and general shape of the scales. However, besides the unique combination of characters mentioned above, *Senekichthys* possess the following characters, which are not found in the elonichthyids and related families referred by Kazantseva-Selezneva (1977; 1981a; 1981b) to the superfamily Elonichthyoidea: absence of laniary teeth, much less oblique suspensorium, absence of ridge scutes, and fulcral scales on the upper caudal lobe ending well before its distal tip. Most (if not all) of the mentioned characters support the derived position of *Senekichthys* in comparison with the Elonichthyidae, which seem to be the most primitive elonichthyiforms (Kazantseva-Selezneva, 1981b), but none of them indicates relationships with other phyletic lineages of the elonichthyiforms of Kazantseva-Selezneva. Thus, *Senekichthys* can be considered as probably deriving from the Elonichthyidae. However, since the structure of the opercular and cheek series of the bones is undeterminable in *Senekichthys*, referral of this taxon to the order Elonichthyiformes (sensu Kazantseva-Selezneva, 1977) and its affinity with the elonichthyids are only putative and based only on the similarities in general appearance, fins position and general shape of the scales between *Senekichthys* and Elonichthyidae. On this ground, it is more justified to classify *Senekichthys* only as Palaeoniscimorpha *incertae sedis*.

Conclusion

Senekichthys hirundo gen. et sp. nov. is characterized by the following unique combination of characters: very long and short-based anal fin; very slim and long scaly caudal lobe, and caudal fin only 1.6 times shorter in length than both the trunk and head; very long but short-based paired fins; long and pointed snout without distinct rostrum; very large orbit being commensurable with postorbital head length and not so far anteriorly placed. It resembles *Dwykia analensis*, the single known species of the family Dwykiidae from the Visean of South Africa, in the characteristic shape of the anal fin, but differs from the latter in the slightly more numerous anal fin rays (approximately 20 vs. approximately 16) and in a more elongated caudal peduncle. Since the only known specimen of *D. analensis* is very incomplete, and there are few reasons for inclusion of the Tuva and the South African forms into a monophyletic lineage, *S. hirundo* is described as a separate genus. In general appearance, fins position and shape of the scales, *Senekichthys* is similar to the family Elonichthyidae, but many derived characters it possesses exclude this new genus from the elonichthyids. As the preservation of the single known specimen of *S. hirundo* is incomplete, this taxon is classified only as Palaeoniscimorpha *incertae sedis*.

Until now the Lower Carboniferous fish beds of Tuva remain very poorly known, however, they contain perhaps a very rich and interesting fish fauna. The Lower Tournaisian fishes of Tuva belong to the endemic lacustrine fauna of Western Siberia, while the Upper Tournaisian complex is similar to Upper Tournaisian-Visean fish faunas of South Africa and West Europe.

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