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**NEW FLYING REPTILES FROM THE MESOZOIC
OF KAZAKHSTAN AND KYRGYZSTAN***

During the collection of fossil insects in the Jurassic lake sediments of Karatau (Kazakhstan) and in the Triassic river sediments of Ferghana (Kyrgyzstan), I found the remains of various small reptiles, among which two belong to flying forms. They have already been briefly reported in press (Sharov, 1966). One of them is a rhamphorhynchoid from the family Dimorphodontidae, the other is a representative of a new family from the order Pseudosuchia.

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NEW RHAMPHORHYNCHOID FROM THE UPPER JURASSIC OF KARATAU

The remains of pterosaurs are very rare on the territory of the USSR. Only fragmentary remains of the rhamphorhynchoid *Batrachognathus volans* Riabinin (Ryabinin 1948) are known from the Jurassic deposits of Karatau. In addition to another specimen of this species, another rhamphorhynchoid was found in the same deposits, which is described below.

ORDER RHAMPHORHYNCHOIDEI

FAMILY DIMORPHODONTIDAE SEELEY, 1870

Genus *Sordes* Sharov, gen. nov.

Genus name from *sordes* — *Latin* — devil.

Type species — *Sordes pilosus* sp. nov.

Diagnosis. The length of the skull exceeds the height by about 3.5 times. No more than seven pairs of teeth in the upper jaw and six pairs in the lower jaw. The lower jaw teeth except the anterior pair are tilted back, the upper jaw teeth tilted forward. The trunk is short, no longer than the forearm and wrist combined. The cervical vertebrae are massive, their width is 1.5 times their length.

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The cervical ribs are longer than the cervical vertebrae. The humerus is longer than the femur, almost straight along the outer edge. The deltoid process of the humerus does not exceed its thickness at mid-length and is not separated by a notch from the head of the humerus. The bones of the forearm are more than 1.5 times longer than the shoulder bones. The metacarpal bone of the wing finger is less than twice as thick as the other metacarpal bones. Fingers I–III of the wings are equal in length. The claws are thin, sharply curved, with a deep notch along the inner edge. Any of the phalanges of the wing finger is much shorter than the forearm. Ilii are narrow, more than twice as long as the ischia. Prepubic bones are narrowed at the front and form a short symphysis. Their lateral edges are protruding. The metatarsal bone of digit V is pear-shaped. Digit V in the extended state reaches the base of the ungual phalanges of digits I–IV. The tail is much longer than the wing finger, slightly flattened and expanded along the distal 1/4 of the length. The diamond-shaped tail vane, characteristic of *Rhamphorhynchus*, is absent.

Species. Type species.

Comparison. According to the small number of teeth, massive cervical vertebrae, short body, relative length of the shoulder, forearm and phalanges of the flying finger, weak development of the metacarpal bone of the wing finger, narrow and forward-reaching ilia, short symphysis and the presence of lateral protrusions in the prepubic bones, the genus *Sordes* is close to the genus *Scaphognathus* Wagner, 1861, from the Upper Jurassic slates of Bavaria (Solnhofen), from which it differs by a less curved humerus, with a shorter deltoid process that is not separated by a notch, equal in length to the fingers I–III of the forelimb, thinner and longer claws of the fingers, a shorter femur compared to the humerus, and narrower prepubic bones, the lateral protrusions of which are located further from the symphysis.

Sordes pilosus Sharov, sp. nov.

Fig. 1-2; Table IV, fig. 1, Table V, fig. 1-2

Species name from pilosus – Latin – hairy.

Holotype — PIN No. 2585/3; almost complete skeleton with preserved impressions of body integument and flying membrane; Mikhailovka (Aulie), Algabas district, Chimkent region of the Kazakh SSR, 100 km north of the city of Chimkent; Upper Jurassic; Table IV, fig. 1; Table V, fig. 1.

Diagnosis. The pre-ungual phalanx of finger I is longer than those of fingers II and III. Claws are shorter than pre-ungual bones. The metatarsal bones of digits I–III are equal in length. The pre-ungual phalanges of toes II–III are of the same length.

Dimensions (in mm). The length of the holotype skull is about 80, the height at the border of the orbital and pre-orbital fenestrae is 20, the width of the lower jaw at the same level is 5. The trunk length is 90, the shoulder blade is 24, the coracoid is 22, the humerus is 40, the forearm is 68, the carpus is 15, pre-ungual phalanges of fingers I–III are 11, 9, 8, respectively; phalanges I–IV of the wing finger are 46, 52, 52 and 33 respectively. Wingspan is about 700–760. The length of the ilia is 30; the distance from their anterior ends to the center of the acetabulum is 21. The length of the femur is 33, the lower leg is 50, the foot is 35, the metatarsal bones of digits I–III are 14, the pre-ungual phalanges of the same digits are 9, the same for digits IV are 12 and 6. The lengths of phalanges 1–3 of digit V are 10, 7 and 7, respectively. Tail length is 220, the thickness at the middle of its length is 2.5, at the end — up to 5.

Notes. *S. pilosus* is interesting primarily because, thanks to the fine-grained rock in which it was enclosed, in addition to the skeleton, the imprint of the body integument and wing membranes were preserved. *S. pilosus* had a thick hairy coat (Table IV, fig. 1; Table V, fig. 1a). Although the presence of filaments in *Rhamphorhynchus* has been noted before (Goldfuss, 1831; Broili, 1927), a complete picture of its density, distribution on the body and appendages is given for the first time by *S. pilosus*. A long, dense covering of rather thick hair is seen over the entire body, and the curvature of individual hairs and tufts shows that they were quite elastic. Hair was also present on the wing membrane, fingers, and the membranes between the toes, although it was sparser and shorter there. The base of the tail was also covered with hair, but the rest of it was apparently naked. The longest hair covering the body reached 6 mm.

The good preservation of the wing membrane impression allows to trace its exact boundaries (Fig. 1; Table V, fig. 1a). The trailing edge of the wings, when spread out, was located posterior to the base of the tail at a distance approximately equal to the length of the lower leg. Thus, in *S. pilosus*, the wing width was at least as wide as in pterodactyls (Fig. 2) and significantly larger than in previous *Rhamphorhynchus* reconstructions (Broili, 1927; Brown, 1943; Augusta, Burian, 1961). The trailing edge of both wings was uniform, and, apparently, only when the wings were folded, the border of the right and left wings can be determined by a small notch, which is marked with an arrow in the photo (Table V, fig. 1a) and Figure 1. At this point, the membrane is covered with more frequent and coarse hairs. No folding trace is observed in this place.

It is interesting to note that the tail is displaced from this notch to the left, and nothing implies that it was torn from the membrane. This shows that in rhamphorhynchoids the tail was separated from the wing membrane. Since the tail served as a balance beam and rudder, such separation seems quite reasonable.

The main support for the wing membrane, in addition to the fingers, were legs. In the holotype, the thighs and lower legs, bent at right angles (Fig. 1), are located entirely in the area of the membrane. Apparently, this is the position they occupied during flight. When the wings were folded, the folds were formed on both sides of the recess, visible as two dark protrusions located symmetrically from the median recess, at the base of the feet. Apparently, when moving on the substrate, the membrane in these folds was somehow protected from damage. It is possible that the hook-shaped digit V served for this purpose, the function of which is considered to be the support and stretching of the trailing edge of the wing membrane during flight (Khozatsky, Yuryev, 1964). In the holotype of *S. pilosus*, the phalanges of this digit on both legs are oriented in the same way: from the short pear-shaped metacarpal bone, the long 1st phalanx extends obliquely along the back of the metacarpal bones of digits I–IV; at a sharp angle to it is the 2nd phalanx, also passing along the back of the wrist, and the 3rd, devoid of a claw, passes at an obtuse angle to the last almost parallel to the 1st phalanx. Apparently, this was also the life position of the phalanges of this finger, which with its hook squeezed and fixed the fold of the wing on the back of the foot. The absence of a claw also seems to be directly related to this function, for the claw could have damaged the wing membrane.

The structural features of the wings of rhamphorhynchoids indicate that these animals still possessed imperfect flight, and they were probably mainly gliding forms. This is confirmed not only by the large surface of the wings, but also by the presence of a long tail, which is typical only for

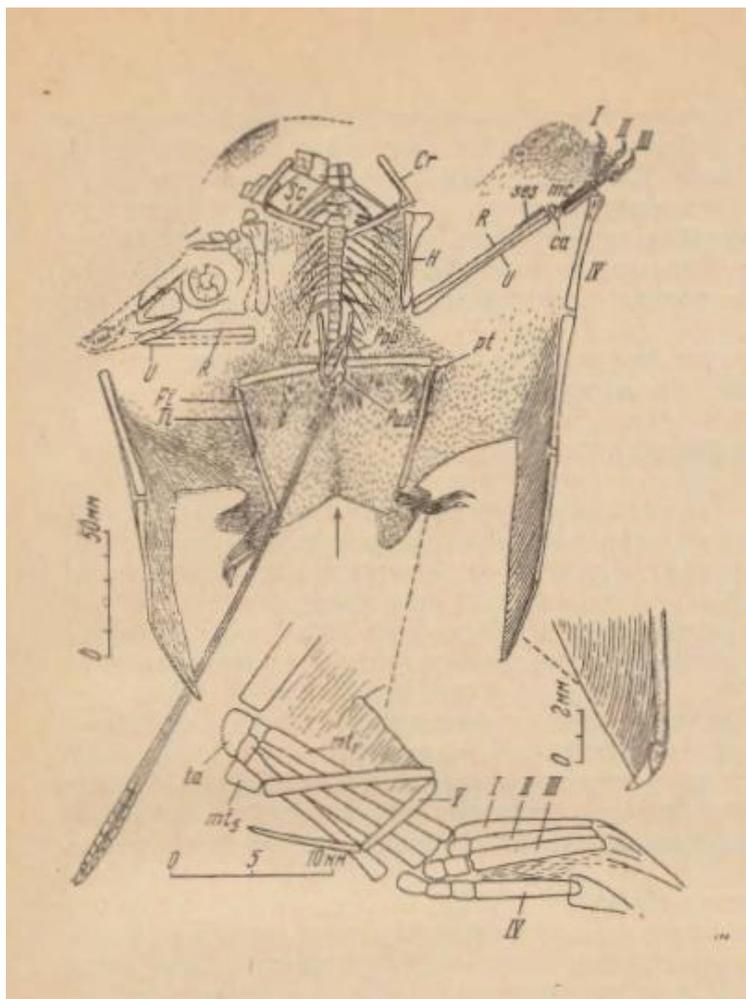


Fig 1. *Sordes pilosus* sp. nov.
Holotype, No. 2585/3; details of the limb structure

- ca — carpal bones;
- Cr — coracoid;
- Fi — fibula;
- H — humerus;
- Il — ilium;
- mc — metacarpal or metacarpal bones;
- mt — metatarsal or metatarsal bones;
- Pub — pubic bone;
- Ppb — prepubic bone;
- pt — knee bone;
- R — radius;
- Sc — scapula;
- Ses — sesamoid bone;
- ta — tarsal bones;
- Ti — tibia;
- U — ulna;
- I-V — phalanges

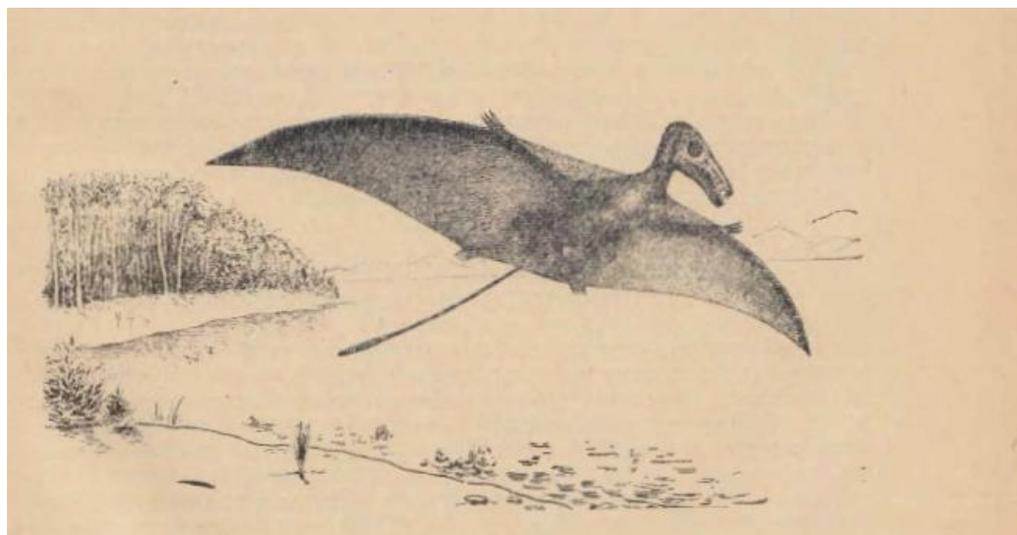


Fig. 2. Life restoration of *S. pilosus* sp. nov.

gliding animals. *Archaeopteryx*, which was capable only of gliding, had a long tail. Among the insects, the gliders were Palaeodictyoptera, which also had long tail appendages (cerci). In pterodactyls, the improvement of the flying organs and the transition to active flight caused the reduction of the tail and the fifth toe, which supported the membrane during gliding. Interestingly, in insects, the origin of active flight was accompanied by a reduction of the tail appendages.

Between toes II and III, there is an impression of a membrane covered with sparse hair. The widespread belief that *Rhamphorhynchus* could swim is hardly justified. A massive head with a short body, long wings, and a tail could hardly be present in floating forms, especially since getting wet would dramatically reduce the aerodynamic qualities of the wings. The membrane between the fingers, apparently, served not for swimming, but for support when moving on shallow muddy ground, which, by the way, was very common along the shoreline of the Jurassic Lake Karatau, including at the point where the remains of rhamphorhynchoids were found (Gecker, 1948). It is possible that the membranes increased the surface of the body during flight, and also served as rudders.

The new species gives an idea of some interesting features of the structure of the skeleton of rhamphorhynchoids. It turned out that they have a short fifth phalanx and a wing finger claw (Fig. 1; Table V, fig. 16). This phalanx and claw were previously thought to have disappeared in pterosaurs. At least three proximal caudal vertebrae carry transverse processes.

As noted by T. Edinger (Edinger, 1927) and O. Kuhn (Kuhn, 1963), the brain of pterosaurs was already as advanced as that of extant birds, whereas the Upper Jurassic *Archaeopteryx* had a brain still typical of reptiles. In pterosaurs, the bones were already pneumatized. The presence of hair, as noted by many researchers, indicates that pterosaurs were warm-blooded. Qualitatively, pterosaurs are no less, and perhaps even more, separated from reptiles than *Archaeopteryx*. According to Kuhn, pterosaurs do not strictly belong in Reptilia. It seems to me that there is every reason to raise the taxonomic rank of Pterosauria, i.e. to allocate them to a separate class (Kuhn, 1967).

Materials. In addition to the holotype, one incomplete skeleton with an impression of the integument from the same location, No. 2470/1 (Table V, fig. 2), which differs from the holotype only by a slightly smaller size (by 1/10) and probably belonged to a juvenile.

A PECULIAR FLYING REPTILE FROM THE LOWER TRIASSIC OF FERGHANA

The sediments of the Madygen Formation, in which the reptile described below is found, are apparently riverine. Together with the remains of three other reptiles, numerous plant remains, mainly horsetails, various paleoniscoid fish, one species of lungfish (Vorobyova, 1967), and a large number of insect prints were found in the same sediments. According to T. A. Sixtel (1962, p. 285), "morphological features of the Madygen-age plants allow us to assume that they grew in a continental climate with fairly sharp seasonal changes." The remains of the reptile were encased in a fine layered clay deposit, which preserved not only the skeleton, but also the impression of body integuments and its appendages. Unfortunately, apparently, during the burial, the head turned around its axis by 180°, as a result, the skull (Fig. 4, A; Table VI, fig. 16) is oriented by the ventral surface, although the

animal's body is visible from the dorsal view. It is impossible to prepare the dorsal skull side due to the crushing and crumpling of the bones from to the compression of the rock. The pelvis structure, however, was studied in more detail. The far-reaching ilia indicate that this reptile most likely belongs to the order Pseudosuchia.

ORDER PSEUDOSUCHIA

FAMILY PODOPTERYGIDAE SHAROV, FAM. NOV.

Type genus – *Podopteryx* gen. nov.

Diagnosis. The head is elongated, pointed at the end; its length exceeds the width by more than three times. Orbits are large. Neck is long, about 2/3 of body length. Seven cervical vertebrae. Cervical ribs are long. The transverse processes of the trunk vertebrae are equal to or even greater than the width of the vertebrae. Gastralia are present. Dorsal ribs are not found; they are either not preserved, reduced, or indistinguishable from the abdominal ones. Forelimbs are relatively short: the shoulder and forearm together are shorter than the distance from the shoulder to the hip joint. Iliac are broad, extending far forward parallel to the spine. Pre-acetabular process present. The limb bones are pneumatic. Fibula and tibia are long; each is equal to or greater than the distance from the shoulder joint to the hip joint. Femur bears a process on the distal end. The fibula is very thin, fused with the tibia. The metatarsals are relatively short, more than 4 times shorter than the ankle. The first toe is shortened, but not lost. The tip of the claw reaches the middle of the first phalanx of the second digit. Digit IV is the longest. The tail is long, at least 1.5 times longer than the head, neck, and trunk combined; thick at the base, with broad vertebrae, the transverse processes of which are directed obliquely back. Starting from the 10–11th vertebrae are devoid of processes, their length is 2–3, and by the end of the tail 5–7 times more than the width. There are more than 30 tail vertebrae. There is a membrane between the shoulder, thigh, and trunk, as well as between the thigh, shin, and base of the tail. Between the shoulder, hip and torso, it was reinforced with thin integumentary bones similar to abdominal ribs.

Comparison. In terms of the unusually long hind legs, long tail, the fusion of the fibula with the tibia, and the pneumaticity of the limb bones, the Podopterygidae are close to the Scleromochlidae Woodward from the Upper Triassic of England, from which they differ in a longer head and neck, shorter metatarsal bones, and a less reduced first digit of the hind limbs.

Notes. The presence of a flying membrane between the hind legs and the base of the tail, and the transformation of the hind limbs into wings is striking in its strangeness. Woodward (1907) suggested that *Scleromochlus* was adapted to running or jumping on its hind legs. Later, F. Huene (1914) suggested, which was then mentioned in the reviews (Khozatsky and Yuryev, 1964; Hoffstetter, 1955; Romer, 1966), that the light body and limbs adapted to climbing and jumping indicate the ability of *Scleromochlus* to parachute. Huene believed that *Scleromochlus* had a fold of skin on the forelimbs and elsewhere, but he apparently had not the slightest idea that such a fold could be between the hind limbs and the base of the tail. However, judging by the structure of the hind legs of *Scleromochlus*, it is more likely that it, like *Podopteryx*, had the same membrane, although it probably was less capable of flight.

Scleromochlus is sometimes regarded as the closest relative of pterosaur ancestors. Now, after the discovery of *Sordes pilosus*, it is clear that the evolution of pterosaurs went in a different direction than the evolution of Podopterygidae and Scleromochlidae. In pterosaurs, the hind limbs did not undergo elongation to the same extent as in representatives of these two families. The thigh and lower leg are much shorter than the trunk, and the end of the thigh, which is drawn forward, does not reach the level of the shoulder girdle. In pterosaurs, the forelimbs were elongated, mostly the forearm and digit IV. Toe I, which is well developed in pterosaurs, is shortened in Podopterygidae and Scleromochlidae. On the contrary, finger V, which the posterior edge of the membrane was attached to in Podopterygidae, is less developed in pterosaurs (rhamphorhynchoids), free, and serves to stretch and support the membrane. The metatarsal bone of digit V in pterosaurs is short, while in Scleromochlidae and Podopterygidae it is long. Finally, unlike Podopterygidae, and probably Scleromochlidae, the flying membrane of pterosaurs was separated from the tail. Thus the flying apparatus of Podopterygidae and Scleromochlidae was formed by different components than in Pterosauria. This is another variant of the flying apparatus that evolved independently in this group of Triassic reptiles, although it is possible that they had common ancestors with pterosaurs that possessed a rudimentary flying membrane between the body, forelimbs and hind limbs.

Another variant of the apparatus, similar to that of modern lizards of the genus *Draco* (Fam. Agamidae), where the membrane is stretched between elongated dorsal ribs, is described from the Upper Triassic of England (Robinson, 1962, 1967) and North America (Colbert, 1963, 1966) in lizards of the family Kuehneosauridae Kuhn, 1964, and the postcranial bones of representatives of this family were not pneumatic. However, as both authors note, there is no phylogenetic relationship between Kuehneosauridae and *Draco*. In Kuehneosauridae, all the dorsal ribs are elongated and stretch the membrane, whereas in *Draco*, only a few presacral ribs serve this purpose. Thus, in the evolution of reptiles, there were at least five variants of winged forms, of which only one, represented in birds, turned out to be the most perfect, manifested as an aromorphosis.

Genus *Podopteryx* Sharov, gen. nov.

Genus name from podes – Greek – leg, pteros – Greek – wing.

Type species – *P. mirabilis* sp. nov.

Diagnosis. The posterior processes of the hyoid apparatus are long, making up 2/3 of the greatest width of the head. The metatarsal bone of digit V of the hind legs is 3 times longer than the first phalanx of the same finger. The latter is equal in length to the second phalanx. The transverse processes of the second postsacral vertebra are directed backward.

Species. Type species.

Podopteryx mirabilis Sharov, sp. nov.

Fig. 3–5; Table VI, fig. 1

Species name is from mirabilis – Latin – amazing.

Holotype — PIN No. 2584/8; skeleton and impression of the wing membrane and part of the skin of almost an entire animal; Djailaicho locality, Madygen tract, Lyailak district, Osh region,

Kirghiz SSR; Lower Triassic, Madygen Formation, upper strata; Table VI, fig. 1.

Description. The ankle is 1.3 times longer than the thigh. The distance between the acetabulum is equal to the greatest width of the head. Toe V is shorter than the third. The longest tail vertebrae are equal in length to the longest neck vertebrae. The holotype has an impression not only of the flying membrane, but also of the skin covering the head, neck, limbs, and base of the tail. The skin bore small scales of the same type as those of modern lizards. The larger scales formed a frill on the sides of the shins, as well as a low ridge on the dorsal side along the base of the tail. This ridge apparently extended to the torso as well.

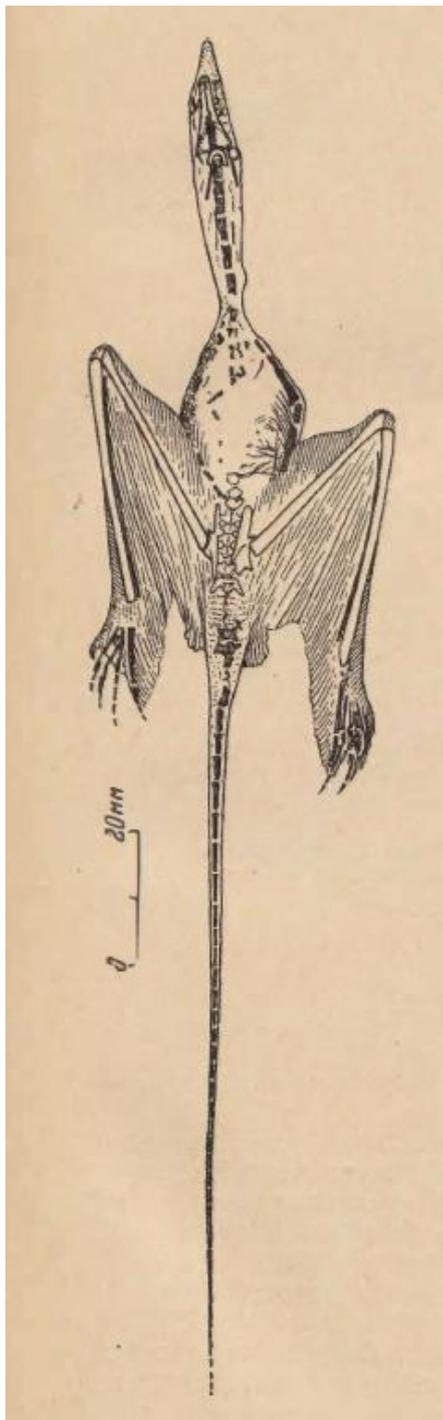
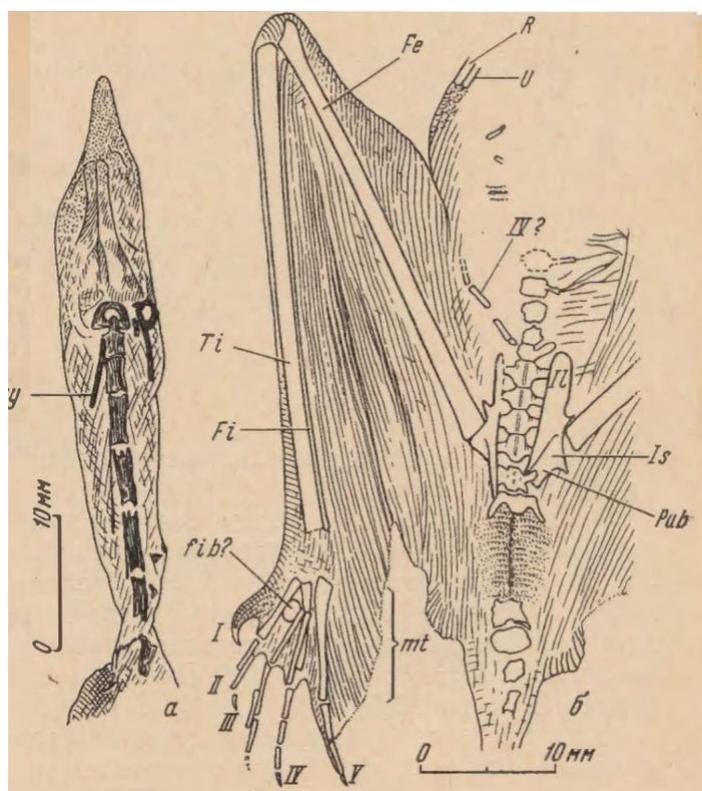


Fig. 3. *Podopteryx mirabilis* sp. nov. Holotype, №2584/8; general view

Fig. 4. *P. mirabilis* sp. nov. Anatomy details
 a — head and neck;
 b — part of the torso, left leg, pelvis and base of the tail
 Fe — femur;
 fib — calcaneus;
 hy — hyoid apparatus;
 Is — ischium (other designations are the same as in Fig. 1)



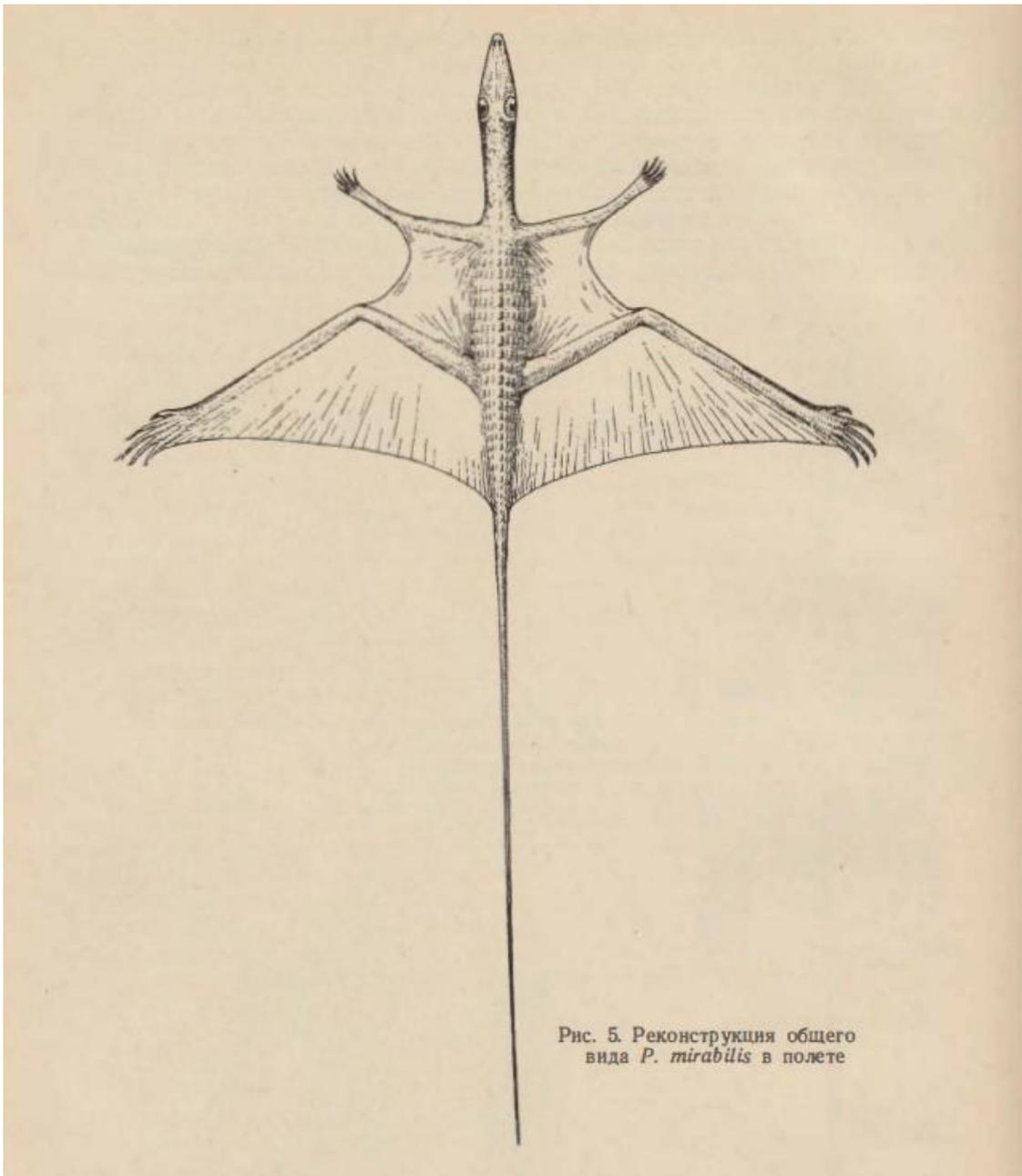


Fig. 5. Life restoration of a flying *P. mirabilis*

Dimensions (in mm). The length of the body from the end of the snout to the base of the tail is 80. Head length 20, maximum width 6. Neck length is 25, trunk length is 35, the length of the preserved part of the tail is 118, estimated tail length is 130–140, shoulder is 12, forearm is 12, ilium is 9.2. Thigh length 33, lower leg 37, metatarsals of digits I–V are 5.0; 5.8; 7.0; 7.0; 9.0 respectively. The length of fingers I–V is 4.8; about 10; about 12.0; 14.8; 8 respectively.

Paleoecology. Features of the limb structure suggest that *Podopteryx* was a forest dweller.

Its small size suggests that it most likely fed on small insects. When the animal noticed an insect flying by or crawling on a branch, it made a short jump and spread its front and hind legs to the sides (Fig. 5). In the same way, it could fly from branch to branch, with the membrane allowing to glide, lengthening the jump, and the tail served as a counterweight for the head and torso, and possibly the rudder.

Materials. Holotype.

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EXPLANATIONS TO TABLES*

Table IV

Fig. 1. *Sordes pilosus* sp. nov., holotype, No. 2585/3, Mikhailovka locality, Upper Jurassic, x0.56

Table V

Fig. 1. *Sordes pilosus*, details of the structure

a – hind limbs, base of the tail, membrane of the wings and hairline; x0.95. The arrow indicates the junction of the membrane of the left wing to the right wing; b – the top of the right wing, x1.3

Fig. 2. The same, paratype, No. 2470 1, from the same locality, x0.49

Table VI

Fig. 1. *Podopteryx mirabilis* sp. nov., holotype. No. 2584/8, Djailaicho; Lower Triassic 1a – x0.85; 1b – x3.2; 1e – x3.2

*) Originals of all tables, except Tab. XI and XII, are stored in the Paleontological Institute of the Academy of Sciences of the USSR