

# The Age of Dinosaurs in Russia and Mongolia

EDITED BY

Michael J. Benton  
University of Bristol

Mikhail A. Shishkin  
Palaeontological Institute, Moscow

David M. Unwin  
Humboldt University, Berlin

Evgenii N. Kurochkin  
Palaeontological Institute, Moscow



CAMBRIDGE  
UNIVERSITY PRESS

# Enigmatic small reptiles from the Middle–Late Triassic of Kirgizstan

DAVID M. UNWIN, VLADIMIR R. ALIFANOV AND MICHAEL J. BENTON

## Introduction

Thick sequences of fluvial and lacustrine deposits at Madygen in Fergana, Kirgizstan provide an unparalleled record of Middle–Late Triassic continental floras and faunas of Middle Asia (Dobruskina, 1995). In addition to a wealth of plant fossils, these sediments have also produced vertebrate material, including the remains of two small diapsid reptiles, both discovered in 1965 by A.G. Sharov during expeditions organized by the Palaeontological Institute, Moscow, to collect fossil insects (Sharov, 1966). Rapid burial of the carcasses in fine-grained sediments led to the preservation of some integumentary structures.

One specimen, preserved with evidence of the integument and extensive flight membranes associated with the hind limbs, was named *Podopteryx* ('foot-wing') by Sharov (1971a). It was later (Cowen, 1981) renamed *Sbaroviptyx*, since *Podopteryx* was found to be pre-occupied. Sharov interpreted *Sbaroviptyx* as a small arboreal glider, an idea that was enthusiastically taken up by others (e.g. Halstead, 1975, 1982), as well as Gans *et al.* (1987), who redescribed *Sbaroviptyx*. Initially, *Sbaroviptyx* was thought to be a pseudosuchian (Sharov, 1971a) and possibly ancestral to pterosaurs (Halstead, 1975, 1979, 1982, 1989). Later, Gans *et al.* (1987) suggested that it may be a more primitive diapsid, an idea supported by Tatarinov (1989, 1994), who identified *Sbaroviptyx* as a prolacertiform.

The second diapsid to be described from Madygen, *Longisquama insignis* (Sharov, 1970), is known from less complete material, but sufficient is preserved to show that this extraordinary animal bore a row of elongate frond-like scales upon its back. The anatomy and

function of these structures remains unclear: Sharov (1970) supposed that they acted as parachutes, while Halstead (1975) and Haubold and Buffetaut (1987) suggested that they could be deployed laterally to form flight surfaces. *Longisquama* was identified as a pseudosuchian by Sharov (1970), but this idea has not yet been critically assessed.

## Repository abbreviation

PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow.

## Geology

Both taxa were found at site 14 of Dobruskina (1995, fig. 9, T-14), at Dzhailyau-Cho, in the Madygen area, Lyailyakskii district, Osh Province, southern Fergana, in Kirgizstan (Figure 10.1). The remains were discovered in sediments of the Madygen Svita, a series of lacustrine and fluvial deposits about 500 m thick, consisting of intercalated sands, silts, and clays with discontinuous coal seams (Dobruskina, 1995). The Madygen Svita was previously thought to be Early Triassic (Sharov, 1970, 1971a), but more recent studies based on the extensive flora indicate a Middle or Late Triassic (Ladinian–Carnian) age (Dobruskina, 1970, 1976, 1980; Vakhrameev *et al.*, 1978). Dobruskina (1980) equates the flora with the Laurasian *Scytrophyllum* flora, derived from the Keuper strata of the Germanic basin.

*Sbaroviptyx* and *Longisquama* were recovered from compact, light grey-yellow bedded shales in the 'upper member' of the Madygen Svita, about 50 m

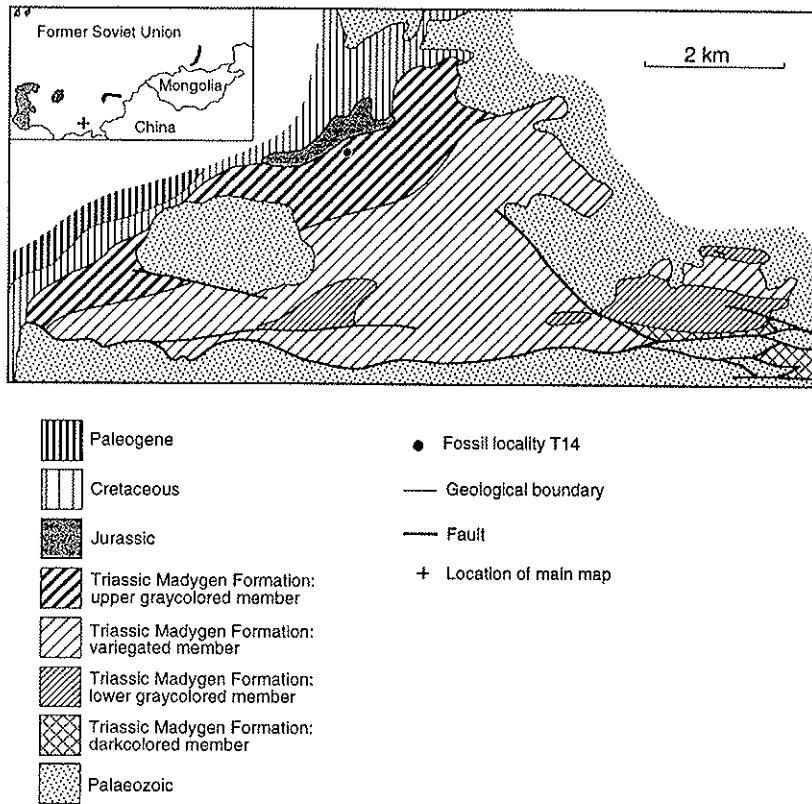


Figure 10.1. Geological map showing the site of discovery of *Sharovipteryx* and *Lougisquama*. Inset, geographic location of main map. (Redrawn from Dobruskina, 1995.)

below the top of the unit (Dobruskina, 1995; Figure 10.1). Associated fossils include abundant plants, predominantly ferns, lycophytes, horsetails, cycads, ginkgos, and conifers (Dobruskina, 1995), bivalves, crustaceans, numerous insects, fishes, including the dipnoan *Asiatoceratodus* (Vorob'eva, 1967) and the saurichthyiform *Saurichthys* (Dobruskina, 1995), as well as a variety of other actinopterygians (Selezneva and Sychevskaya, 1989), a small poorly-preserved tetrapod, *Triassurus*, described as the earliest urodele (Ivakhnenko, 1978), and the skeleton of a cynodont, *Madygenia* (Tatarinov, 1980, 1994).

### Systematic survey

Subclass DIAPSIDA Osborn, 1903  
 Order PROLACERTIFORMES Camp, 1945  
 Family PODOPTERYGIDAE Sharov, 1971a  
 (= SHAROVIPTERYGIDAE Tatarinov, 1989)  
*Sharovipteryx mirabilis* (Sharov, 1971a)

See Figures 10.2 and 10.3.

*Diagnosis.* Pronounced caudal elongation of hyoids. Anterior development of preacetabular process of ilium. Process on distal end of femur; elongation of tibia, which is longer than the trunk. Sharov (1971a, p. 108) and Tatarinov (1989) cited long lists of supposedly diagnostic characters, but many of these are also

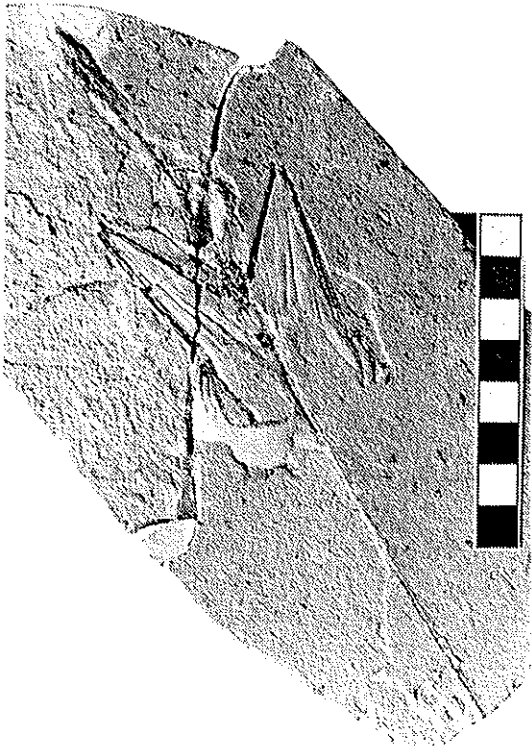


Figure 10.2. Holotype of *Sbarovipteryx mirabilis* (PIN 2584/8), main slab. Scale bar divided into centimetres.

found in other diapsids. Tatarinov (1989) claimed that the relative shortness of the fore limbs, only one-third or one-quarter the length of the hind limbs, was also diagnostic of *Sbarovipteryx*, but as the forelimbs have yet to be clearly identified this cannot be substantiated.)

*Material and preservation.* *Sbarovipteryx* is represented by a single specimen, the holotype (PIN 2584/8), borne upon a slab and counterslab (Sharov, 1971a; Gans *et al.*, 1987). The skeleton is largely complete and almost fully articulated, though crushed in places. The skull is considerably compressed and visible in dorsal view, not ventral as Sharov (1971a) supposed (Gans *et al.*, 1987). The tip of the tail is lacking, but otherwise the spinal column is complete, though parts are not

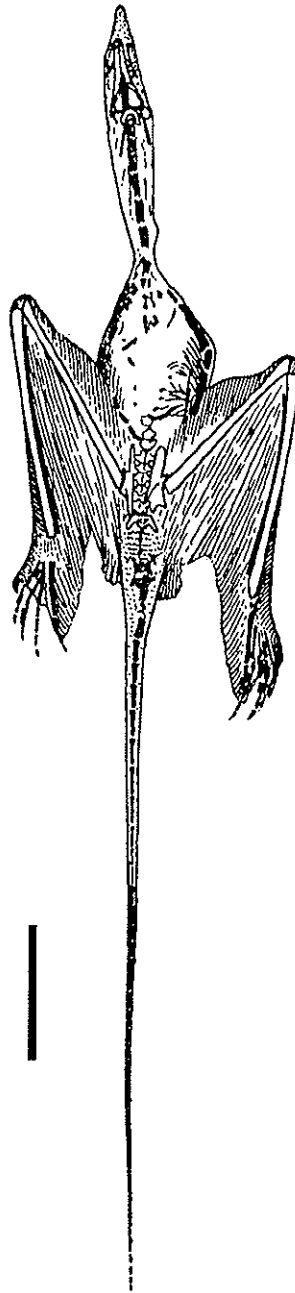


Figure 10.3. Preserved remains of the skeleton and impressions of the soft tissues of *Sbarovipteryx*. Scale bar, 20 mm.

well preserved. If present, the forelimbs must be buried within the main slab, since structures previously identified as forelimb elements by Sharov (1971a) and Gans *et al.* (1987) are almost certainly remains of ribs. The hind limbs are largely complete, though the ankles and feet have become disarticulated. Impressions of skin bearing scales are common in the skull area, axial regions of the body, and around parts of the hind limbs. There are also extensive areas of sediment adjacent to the skeleton which bear superbly preserved impressions of flight membranes.

*Anatomy.* *Sharovipteryx* is a small animal with a snout-vent length of about 90 mm and a total body length of no more than 240 mm. Principal features include a narrow, deep skull with large orbit, a long neck and tail, remarkably elongate hind limbs and extensive flight membranes (Sharov, 1971a; Gans *et al.*, 1987).

The skull is narrow and deep with an elongate snout and large orbits located at about mid-length. There appear to have been upper and lower temporal openings, the typical diapsid condition, but the lower margin of the lower opening is obscured by the ramus of the lower jaw and its supposed absence (Gans *et al.*, 1987; Tatarinov, 1989) cannot be confirmed. The upper jaw contains at least 15 teeth per side. Each tooth is narrow, thin, sharp and very gently recurved. The mandible is shallow with long retroarticular processes and long posterior branchial cornua project caudally from beneath the rear margin of the skull.

The neck is equivalent in length to the trunk and composed of at least seven cervicals. Vertebrae three to seven are elongate, with low spinous processes and highly elongate spinal ribs. The sacrum consists of at least four, and possibly as many as six, vertebrae. The tail is very long (more than  $1.5 \times$  snout-vent length) and consists of at least 30 elements, the more distal of which are highly attenuate with lengths up to seven times their breadth. Gastralia, consisting of very thin fine rods of bone, are present in the trunk region.

Previous authors refer to the shoulder girdle (Sharov, 1971a) and very small forelimbs (Sharov, 1971a; Gans *et al.*, 1987; Tatarinov, 1994), but it is not clear to which elements they were alluding. A single

crescent-shaped bone lying to the left of the rostral end of the dorsal series might be remnants of a coracoid, but slender ossifications to the right of the dorsal series, identified by Sharov (1971a) as parts of the forelimb, appear to be the shafts of anterior dorsal ribs. Since the remains are not preserved on a single plane, but project into the sediment, we suppose that the forelimbs are buried within the main slab or, less likely, in the counterslab.

The ilium is remarkable for its elongate anterior process, but much of the rest of the pelvis is buried within the slab and few details are visible. Gans *et al.* (1987) refer to a possible epipubic element, but the identity of this structure is unclear and it might be a disarticulated rib.

The femur is remarkably long, reaching a length equivalent to that of the trunk, but straight, and with an unusual pulley-like process projecting from the distal end. The crus is also elongate, and slightly longer than the femur. The fibula is very slender, but reaches the ankle and is distinct from the tibia, except at the proximal end where the two appear to be fused.

Little remains of the ankle, except for a few disarticulated, isolated elements of uncertain identity. The metatarsus is short, only 25% the length of the femur. The pes contains five digits with a phalangeal formula of 2, 3, ?4, 2+, ?3. The digits are long and slender with intermediate elements reduced in length and elongate penultimate phalanges. There is an increase in length from the first to fifth digit, but digit one is not appreciably reduced in comparison to the other digits, as previous authors have stated, and digit five is of similar length to digit four. Digit five is unusual in that the first phalanx is equivalent in length to the fourth metatarsal.

Many of the appendicular elements are hollow, with bony trabeculae confined to the articular ends. It has been suggested (Sharov, 1971a) that the smooth inner surface of the bone walls indicates pneumatization of the bones, but pneumatophores are not evident on any element.

Impressions provide evidence of two types of external soft tissue: the integument, which usually bears small scales, or a distinctive diamond-shaped

ornamentation; and wing membranes, impressions of which tend to be smoother and often exhibit folds and fine striae. The integument covering the skull, neck, trunk and extending up to the base of the tail bore small tubercular or keeled scales, while in places impressions of flat, imbricate scales are preserved along the margins of the hind limbs and toes.

The extent of the flight membranes is less certain. A large uropatagium was stretched between the hind limbs, attaching to the base of the tail as far as the seventh vertebra and along the posterior margin of the femur, tibia, and pes to the tip of the fifth toe. Sharov (1971a, fig. 5) also reconstructed a flight membrane attached to the body wall and extending forward from the femur to the fore limb. Though absent from their restoration, Gans *et al.* (1987) refer to 'half-moon'-shaped prefemoral folds, but conclude that these structures were not attached to the humerus. By contrast, Ivakhnenko and Korabel'nikov (1987, fig. 260) accept Sharov's interpretation and even add a further membrane fringing the neck and extending to the base of the skull. New studies of the main slab and counter-slab reveal impressions of a flight membrane anterior to the femur and extending laterally, at least as far as the knee. This observation provides some support for Sharov's reconstruction, but it is not possible to determine whether this membrane attached to the fore limb, or not.

*Functional morphology.* Sharov argued that *Sharovipteryx* was a small arboreal glider that flew from branch to branch using the tail as a counterweight and the head and body as a rudder. This idea has been widely accepted (e.g. Halstead, 1975; Gans *et al.*, 1987; Ivakhnenko and Korabel'nikov, 1987; Tatarinov, 1989; Wellnhofer, 1991), although Gans *et al.* (1987) opted for a somewhat different reconstruction of the flight apparatus, proposing that it consisted solely of a uropatagium, possibly assisted by a small canard wing supported by the fore limbs. Other possible functions of the membranes include camouflage and display (Gans *et al.*, 1987).

*Phylogenetic relationships.* Sharov assigned *Sharovipteryx* to the Pseudosuchia on the basis of a single character: the pronounced anterior development of the pre-

acetabular process of the ilium. The Pseudosuchia at the time was a broad grouping of 'advanced thecodontians', including rauisuchians, phytosaurs, aetosaurs, ornithosuchids, and others, whereas current views (Benton and Clark, 1988; Sereno, 1991) restrict the term to aetosaurs and rauisuchians. Charig *et al.* (1976) and Ivakhnenko and Korabel'nikov (1987) supported the idea of *Sharovipteryx* as an archosaur, as did Halstead, who went further and proposed that it was directly ancestral to pterosaurs (Halstead, 1975, 1979, 1982, 1989), basing this opinion on the presence, in both taxa, of wing membranes. Sharov (1971a) had already supposed a possible sister-group relationship with pterosaurs, but he also saw similarities with *Scleromochlus*, a small Late Triassic ornithodiran, and Benton (1993b, p. 698) listed Podopterygidae in Ornithodira.

Other workers (Gans *et al.*, 1987; Tatarinov, 1989, 1994; Wellnhofer, 1991) assigned *Sharovipteryx* to a much lower position within the diapsid tree. Gans *et al.* (1987) identify either Lepidosauria, or Protorosauria, as likely relatives, while Tatarinov (1989, 1994) argued that *Sharovipteryx* belonged within the Prolacertiformes on the basis of the following skull characters: lack of a preorbital opening, loss of the lower temporal bar, elongation of the nostrils, presence of a rudimentary coronoid process on the mandible, and the absence of a mandibular fenestra. However, only the first and last of these can be safely determined in *Sharovipteryx*, and neither character unites this taxon with prolacertiforms because they represent the primitive condition for diapsids (e.g. Benton, 1985; Evans, 1988; Carroll and Currie, 1991; Laurin, 1991).

Despite these difficulties, comparisons with recent cladistic analyses of diapsid relationships (Benton, 1985; Gauthier *et al.*, 1988; Evans, 1988; Carroll and Currie, 1991; Laurin, 1991; Benton and Allen, 1997) suggest that Tatarinov (1989, 1994) is essentially correct. *Sharovipteryx* exhibits two apomorphies of Prolacertiformes; (i) elongate cervical vertebrae (Benton, 1985; Chatterjee, 1986) with (ii) low neural spines (Benton, 1985; Chatterjee, 1986), and it may have a third: an incomplete lower temporal bar (Gow,

1975; Benton, 1985; Chatterjee, 1986), though this has yet to be confirmed. Other characters found in *Sbarovipteryx* and some, though not all prolacertiforms, include a highly elongate femur (Chatterjee, 1986), tibia slightly longer than femur (Chatterjee, 1986), a feature which is also apomorphic for Ornithodira (e.g. Juul, 1994) and pes digit five with elongate proximal phalanx (Olsen, 1979; Chatterjee, 1986). Of the 48 characters of Prolacertiformes, or clades within Prolacertiformes, listed by Benton and Allen (1997), *Sbarovipteryx* may be coded for eight. Derived prolacertiform characters are (numbers follow the list in Benton and Allen, 1997): cervicals longer than dorsals (19), cervical neural spines long and low (20), cervical ribs long and slender (22), femur straight (38), tibia longer than femur (39), and second phalanx of digit V of the foot long (47). *Sbarovipteryx* codes as primitive for two prolacertiform characters: (?) seven or fewer cervical vertebrae (17), metatarsal IV less than three times the length of metatarsal V (45).

The hypothesis that *Sbarovipteryx* is a prolacertiform, or a close outgroup of Prolacertiformes, is further supported by the presence in *Sbarovipteryx* of apomorphies of Prolacertiformes + Archosauria (Benton, 1985) such as a long snout and narrow skull, recurved teeth, long, thin, tapering cervical ribs, and elongate transverse processes of the trunk vertebrae, but the absence of important archosaur apomorphies including an antorbital fenestra, mandibular fenestra and fourth trochanter on the femur.

? Subdivision ARCHOSAURIA Cope, 1869

Family LONGISQUAMIDAE Sharov, 1970

*Longisquama insignis* Sharov, 1970

See Figure 10.4.

**Diagnosis.** Elongate manus digit four, equivalent in length to the humerus. A series of elongate plume-like appendages inserting along dorsal mid-line of body. Occiput bears two tubercle-like structures. (The first two are clearly diagnostic, and the latter is a further possibility. Sharov (1970) cited numerous supposedly diagnostic characters, but they are present in other taxa.)

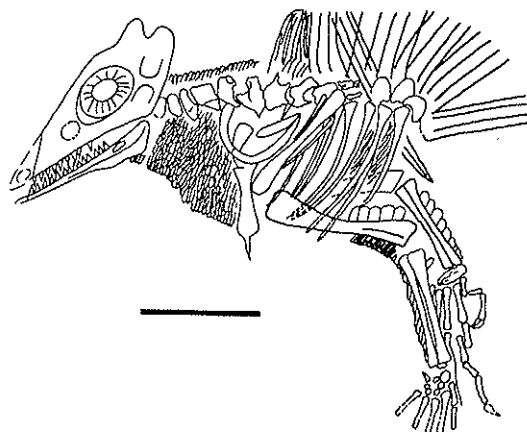


Figure 10.4. Holotype of *Longisquama insignis* (PIN 2584/4), main slab. Preserved remains of the skeleton and impressions of the soft tissues of *Longisquama*. Redrawn from Sharov (1970). Scale bar, 10 mm.

**Material and preservation.** The holotype (PIN 2584/4) consists of an incomplete skeleton, comprising the skull, neck and anterior half of the trunk, the pectoral girdle and forelimbs, and well preserved impressions of the integument. There are a further five specimens consisting of fragmentary remains of the plume-like dorsal appendages. All the remains are heavily crushed and details are poorly preserved.

**Anatomy.** *Longisquama* is a small reptile with a skull about 23 mm long and a total forelimb length of about 44 mm (Sharov, 1970).

The high skull has large orbits, small antorbital openings and, according to Sharov (1970, fig. 1), upper and lower temporal fenestrae. The teeth are small, conical, acrodont, and number 12–13 pairs in the upper jaw and 16–17 in the lower jaw. The neck is short and contains seven cervicals. Only the anterior-most dorsal vertebrae are visible and the rest of the spinal column is not preserved. Long, slender dorsal ribs are preserved in articulation with the trunk vertebrae, but cervical ribs seem to be lacking, though this may be because they are obscured or disarticulated rather than truly absent.

The shoulder girdle is composed of a long, narrow scapula, expanded at both ends, a short, rather rod-like

coracoid, and a long crescent-shaped clavicle which articulates with a well developed interclavicle. The latter element has a rectangular anterior end and a broad stem tapering to a point distally. The humerus is slender, gently sigmoid and of similar length to the radius and ulna, both of which are long, thin and straight. The carpus consists of numerous small indeterminate elements which support five metacarpals. Metacarpals 1–4 are of similar size and about half the length of the forearm, while the fifth is much reduced. The fourth digit appears to contain five phalanges while the fifth has four, thus a phalangeal formula of 2, 3, 4, 5, 4 seems likely. In preserved digits the penultimate phalanx is elongate and supports a sharp-pointed and somewhat recurved claw.

The neck and ventral surface of the thorax appear to have been covered by long, overlapping, simple scales about 0.3 mm wide and up to 1.75 mm long. Similar scales fringe the anterior margin of the humerus and radius. Somewhat larger scales, up to 1.0 mm in width, fringe the posterior margin of the humerus and ulna. The most spectacular structures occur on the dorsal mid-line and consist of a series of paired appendages, apparently one pair per vertebra (Haubold and Buffetaut, 1987). Each paired appendage consists of two long plume-like structures, ranging from 100 to 150 mm in length and about 5–7 times longer than they are wide. The appendages decline slightly in size from front to back, with the longest occurring at the front (Haubold and Buffetaut, 1987). Each plume becomes gently expanded distally and slightly recurved, and is composed of finely folded anterior and posterior margins and a somewhat thickened medial region running from the base to the tip of the plume. Sharov (1970) argued that the paired plumes were joined along their anterior margins, and the posterior margin at the distal tip, but Halstead (1975) and Haubold and Buffetaut (1987) interpret the plumes as separate structures. They are generally thought to have been modified scales (Sharov 1970; Haubold and Buffetaut, 1987), but, unfortunately, they appear to have undergone some postmortem displacement and the nature of their insertion is unclear.

*Functional morphology and ecology.* It seems likely that

*Longisquama* was a small arboreal insectivore (Ivakhnenko and Korabel'nikov, 1987). The numerous short, conical sharp-pointed teeth appear well suited for puncturing and dismembering the chitinous exoskeletons of insects, large numbers of which have already been reported from the Madygen Svita (overview in Dobruskina, 1995). The well developed shoulder girdle and proportions of the main forelimb elements suggest arboreal abilities (Sharov, 1970) and this is further indicated by the presence of elongate penultimate phalanges in the digits, which is a typical feature of climbers (Unwin, 1987, 1988).

The function of the dorsal appendages is uncertain. Sharov (1970) suggested that they might have functioned as parachutes, while Halstead (1975) and Haubold and Buffetaut (1987) went further and proposed that they could have been deployed in such a way as to form aerofoils, enabling the animal to glide from tree to tree. These authors argued that the overlapping plumes formed a flight surface which narrowed caudally, being broadest at the front, and could be raised and lowered by epaxial musculature.

Other functions are also possible. Sharov (1970) suggested that the appendages might have acted as insulation, by trapping air between the plumes, and Halstead (1975) supposed that they could have been erected as a crest and used to frighten predators. In a similar fashion, they would also have been very effective display structures, particularly if brightly coloured.

*Phylogenetic relationships.* Sharov (1970) assigned *Longisquama* to the Pseudosuchia on the grounds that it had an antorbital fenestra and a mandibular fenestra. These characters, if confirmed, would indicate that *Longisquama* belongs within the Archosauria, as others have accepted (e.g. Haubold and Buffetaut, 1987; Witmer, 1991), but they do not support any particular relationship with pseudosuchians (Charig *et al.*, 1976) or other archosaurian lineages. Benton (1993b, p. 698) listed *Longisquama* as an ornithodiran archosaur.

Assignment to Archosauria is problematic, however, since *Longisquama* is also said to have acrodont teeth and an ossified interclavicle, features that are more typical of lepidosaurs. Further, the key archosaur



\*features are not entirely convincing: the antorbital fenestra is not certainly present (Figure 10.4), and the mandibular fenestra is, unusually, shown as located immediately below and behind the mandibular tooth row. It is necessary to show that these two structures do not simply represent damage.

It has been argued by some that birds may be descended from 'pseudosuchians' and, as such, *Longisquama* has occasionally been incorporated into this hypothesis (see Witmer, 1991 for a review). Sharov (1970, 1971b) originated this idea by suggesting that the elongate scales represented an early stage in the evolution of feathers, an idea which was echoed by Halstead (1975) and Bakker (1975). Sharov (1970) also claimed that the clavicles resembled the avian furcula and may even be homologous with this structure. However, soon after *Longisquama* was first described, important new evidence supporting Huxley's contention (1868) that birds were descended from theropod dinosaurs began to emerge (see Witmer, 1991). In light of the widespread acceptance of this hypothesis, and the absence of any further evidence linking *Longisquama* and birds, the idea of *Longisquama* as an avian ancestor can now be safely abandoned.

### Discussion

Diapsids have a good fossil record, but for taphonomic reasons much of it is dominated by medium to very large taxa. Small diapsids are relatively uncommon and examples with soft tissue preservation, such as those from Madygen, are extremely rare. The specimens are important geographically, since these are the only diapsids so far reported from the Triassic of Middle Asia. In addition, if confirmed as Middle-Late Triassic in age, *Sbarovipteryx* and *Longisquama* also fall during an interval of major turnover among terrestrial faunas, when 'Palaeozoic' faunas of synapsids, rhynchosaurs, and basal archosaurs were replaced by 'modern' faunas of dinosaurs, pterosaurs, crocodylomorphs, basal lepidosaurs, turtles, and mammals (Benton, 1993a, 1994).

The Madygen diapsids have been widely ignored. Apart from two functional studies (Gans *et al.*, 1987;

Haubold and Buffetaut, 1987) and a few mentions in the semi-popular literature (e.g. Halstead, 1975, 1982, 1989; Cox, 1988) these taxa have been almost completely ignored and are not even listed in standard compendia such as Carroll (1988). New studies now under way (Unwin, in prep.) and greater ease of access to the original material may rectify this situation.

### Acknowledgements

D.M.U. thanks N.N. Bakhurina, L.P. Tatarinov, V.U. Reshetov, M.F. Ivakhnenko, I.C. Barskov, A.S. Alekseev, and D. Yesin for all their help during his stay in Moscow. D.M.U. is grateful to the British Council for enabling him to carry out extended visits to the Former Soviet Union, and to M. Bird of the British Embassy, Moscow, for his assistance. Many thanks to R.R. Reisz, L.P. Tatarinov and M.F. Ivakhnenko for valuable discussion, to S. Powell (Department of Geology, Bristol University) for the photography, and to G.W. Storrs and M.F. Ivakhnenko for valuable comments on the manuscript. This research was supported by the Department of Geology, Bristol University, and a Royal Society University Research Fellowship awarded to D.M.U.

### References

- Bakker, R.T. 1975. Dinosaur renaissance. *Scientific American* 232: 58–78.
- Benton, M.J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84: 97–164.
- 1993a. Late Triassic extinctions and the origin of the dinosaurs. *Science* 260: 769–770.
- 1993b. Reptilia, pp. 681–715 in Benton, M.J. (ed.), *The Fossil Record 2*. London: Chapman & Hall.
- 1994. Late Triassic to Middle Jurassic extinctions among continental tetrapods: testing the pattern, pp. 366–397 in Fraser, N.C. and Sues, H.-D. (eds.), *In the Shadow of the Dinosaurs*. Cambridge: Cambridge University Press.
- and Allen, J.A. 1997. *Boreoprincea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles. *Palaeontology* 40: 931–953.

- and Clark, J. 1988. Archosaur phylogeny and the relationships of the Crocodylia, pp. 295–338 in Benton, M.J. (ed.), *The Phylogeny and Classification of the Tetrapods. Systematics Association Special Volume, 35A*. Oxford: Clarendon Press.
- Carroll, R. L. 1988. *Vertebrate Paleontology and Evolution*. New York: W.H. Freeman.
- and Currie, P.J. 1991. The early radiation of diapsid reptiles, pp. 354–424, in Schultze, H.-P. and Trueb, L. (eds.), *Origins of the Higher Groups of Tetrapods*. Ithaca, NY: Comstock.
- Charig, A.J., Krebs, B., Sues, H.-D. and Westphal, F. 1976. *Handbuch der Paläoberpetologie. Teil 13, Thecodontia*, Stuttgart: Gustav Fischer, 137 pp.
- Chatterjee, S. 1986. *Malerisaurus langstoni*, a new diapsid from the Triassic of Texas. *Journal of Vertebrate Paleontology* 6: 297–312.
- Cowen, R. 1981. Homonyms of *Podopteryx*. *Journal of Paleontology* 55: 483.
- Cox, C.B. 1988. Amphibians and reptiles, pp. 46–169 in Cox, C.B. (ed.), *Macmillan Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals*. London: Guild Publishing.
- Dobruskina, I.A. 1970. [The age of the Madygen Formation and the Permo-Triassic boundary in Middle Asia.] *Sovetskaya Geologiya* 1970 (12): 16–28.
- 1976. [Correlation of the continental deposits of the Triassic.] *Sovetskaya Geologiya* 1976 (3): 34–45.
- 1980. [Stratigraphic position of the Triassic plant-bearing beds of Eurasia.] *Trudy Paleontologicheskogo Instituta AN SSSR* 346: 1–160.
- 1995. Keuper (Triassic) Flora from Middle Asia (Madygen, Southern Fergana). *Bulletin of the New Mexico Museum of Natural History and Science* 5: 1–49.
- Evans, S.E. 1988. The early history and relationships of the Diapsida, pp. 221–260 in Benton, M.J. (ed.), *The Phylogeny and Classification of the Tetrapods. Systematics Association Special Volume, 35A*. Oxford: Clarendon Press.
- Gans, C., Darevskii, I. and Tatarinov, L.P. 1987. *Sbarovipteryx*, a reptilian glider? *Paleobiology* 13: 415–426.
- Gauthier, J., Kluge, A.G. and Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4: 105–209.
- Gow, C.E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana* 18: 89–131.
- Halstead, L.B. 1975. *The Evolution and Ecology of the Dinosaurs*. London: Peter Lowe, 116 pp.
- 1979. Pterosaurs, pp. 174–176 in Steel, R. and Harvey, A.P. (eds.), *The Encyclopaedia of Prehistoric Life*. London: Mitchell Beazely.
- 1982. *Hunting the Past*. London: Hamish Hamilton, 208 pp.
- 1989. *Dinosaurs and Prehistoric Life*. London: Collins, 240 pp.
- Haubold, H. and Buffetaut, E. 1987. A new interpretation of *Lougisquama insignis*, an enigmatic reptile from the Upper Triassic of Central Asia. *Comptes Rendus de l'Academie des Sciences Paris, Série II* 305: 65–70.
- Huxley, T.H. 1868. On the animals which are most nearly intermediate between birds and reptiles. *Geological Magazine* 5: 357–365.
- Ivakhnenko, M.F. 1978. Tailed amphibians from the Triassic and Jurassic of Middle Asia. *Paleontologicheskii Zhurnal* 1978 (3): 84–89.
- and Korabel'nikov, V.A. 1987. [*Life of the Past World*]. Moscow: Prosveshchenie Press, 253 pp.
- Juul, L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana* 31: 1–38.
- Laurin, M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society* 101: 59–95.
- Olsen, P.E. 1979. A new aquatic eosuchian from the Newark Supergroup (Late Triassic–Early Jurassic) of North Carolina and Virginia. *Postilla* 176: 1–14.
- Selezneva, A.A. and Sychevskaya, E.K. 1989. [Triassic fishes from Madygen (Fergana).] *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii* 64: 131.
- Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology* 11 (Supplement to no. 4): 1–53.
- Sharov, A.G. 1966. [Unique discoveries of reptiles from Mesozoic beds of Central Asia.] *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii* 61: 145–146.
- 1970. [Unusual reptile from the Lower Triassic of Fergana.] *Paleontologicheskii Zhurnal* 1970 (1): 127–131.
- 1971a. [New flying reptiles from the Mesozoic of Kazakhstan and Kirgizstan.] *Trudy Paleontologicheskogo Instituta AN SSSR* 130: 104–113.

- 1971b. Den Vorfahren der Vögel auf der Spur. *Presse Sowjetunion* 117: 5–6.
- Tatarinov, L.P. 1980. [Towards a prehistory of mammals.] pp. 103–114 in Sokolov, B.S. (ed.), [*Palaeontology and Stratigraphy, 26th International Geological Congress*]. Moscow: Nauka.
- 1989. [The systematic position and way of life of the problematic Upper Triassic reptile *Sbarovipteryx mirabilis*.] *Paleontologicheskii Zhurnal* 1989 (2): 110–112.
- 1994. Terrestrial vertebrates from the Triassic of the USSR with comments on the morphology of some reptiles, pp. 165–170 in Mazin, J.-M. and Pinna, G. (eds.), *Evolution, Ecology and Biogeography of the Triassic Reptiles. Paleontologia Lombarda, New Series, 2*.
- Unwin, D. M. 1987. Pterosaur locomotion. Joggers or waddlers? *Nature* 327: 13–14.
- 1988. New remains of the pterosaur *Dimorphodon* (Pterosauria: Rhamphorhynchoidea) and the terrestrial ability of early pterosaurs. *Modern Geology* 13, 57–68.
- Vakhrameev, V.A., Dobruskina, I.A., Meien, S.V. and Zaklinskaya, E.D. 1978. *Paläozoische und Mesozoische Floren Eurasiens und die Phytogeographie dieser Zeit*. Jena: Gustav Fisher, 300 pp.
- Vorob'eva, E.I. 1967. [Triassic *Ceratodus* from Southern Fergana with some comments on the systematics and phylogeny of ceratodontids.] *Paleontologicheskii Zhurnal* 1967 (4): 102–111.
- Wellnhofer, P. 1991. *The Illustrated Encyclopedia of Pterosaurs*. London: Salamander, 192 pp.
- Witmer, L.M. 1991. Perspectives on avian origins, pp. 427–466, in Schultze, H.-P. and Trueb, L. (eds.), *Origins of the Higher Groups of Tetrapods*. Ithaca, NY: Comstock.