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Roksana Skrzyczka
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Revision of two relic actinopterygians from the Middle or Upper Jurassic Karabastau Formation, Karatau Range, Kazakhstan

ROKSANA SKRZYCKA

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Three hundred and forty-six articulated fossil specimens of two species from the Middle or Upper Jurassic Karabastau Formation of the Karatau Range (Kazakhstan, Asia) were studied to revise two little-known palaeonisciform fish: *Pteroniscus turkestanensis* and *Morrolepis aniscowitchi*. Detailed morphological analysis shows that *P. turkestanensis*, *Daqingshaniscus longiventralis* and Uighuroniscidae form a closely related group. They are far more distantly related to the Palaeoniscidae than previously inferred. The first detailed scanning electron microscopy of the unique scale cover of *M. aniscowitchi* is presented. *Morrolepis* is found to be devoid of denticles on the surface of the bones, scales and lepidotrichia—so far considered to be a key coccolepidid characteristic. However, it bears exceptionally robust lateral line scales. Comparison of the axial skeletons of *M. aniscowitchi* and *Morrolepis andrewsi* reveals their close affinities within Coccolepididae. The axial skeleton, despite its rare preservation in palaeonisciforms, may be taxonomically informative, at least at the family level. The Karatau palaeonisciforms, being among the youngest examples of basal actinopterygians (persisting in Asia through the late Mesozoic), possess a set of conservative morphological characters that suggest they were relictual taxa by Jurassic times, thus highlighting some freshwater systems as refuges for plesiomorphic taxa.

Key words: Coccolepididae; evolution; fish; freshwater; Palaeonisciformes; anatomy.


Although the fish species from Karatau Range (Karabastau Formation) were named and preliminarily described soon after their discovery (Gorizdro-Kulczycka 1926), they still await modern detailed anatomical description and taxonomic discrimination. There are two Karabastau palaeonisciform species: one historically assigned to the Palaeoniscidae and the other belonging to the Coccolepididae. In some exposures of the Karabastau Formation, the coccolepidid *Morrolepis aniscowitchi* (Gorizdro-Kulczycka, 1926) dominates, whereas in others the palaeoniscoid *Pteroniscus turkestanensis* (Gorizdro-Kulczyka, 1926) is more abundant (Hecker 1948). A list of all actinopterygians recognized in the Karatau fish assemblage was produced by Chang & Miao (2004). Apart from palaeonisciforms, it also includes a ptycholepidid, a chondrostean, a galkiniid and a pholidophorid.

The two species described in this paper, *Pteroniscus turkestanensis* and *Morrolepis aniscowitchi*, are among the youngest representatives of the palaeoniscoids (Palaeoniscimorpha *sensu* Lund *et al.* 1995 or basal Actinopteri *sensu* Patterson 1982). Both species were first described by Gorizdro-Kulczyka (1926). They are classified within the order Palaeonisciformes, traditionally as the suborder Palaeoniscoidei (or Palaeoniscoidea), alongside the deep-bodied Platysomoidei (according to Jarvik 1980), encompassing the least specialized actinopterygian fishes. The Palaeonisciformes includes 27 families according to Romer (1966), and 24 families according to Carroll (1988). Their interrelationships remain obscure (Patterson 1982, Gardiner 1993, Lund & Poplin 2002, Cloutier & Arratia 2004).
Basal actinopterygians are interpreted to represent the morphologically ancestral type of actinopterygian (the palaeopterygian *sensu* Regan, 1923) structure. Their generalized anatomy remains little changed up to the Early Cretaceous as shown by many features of the family Coccolipidae and *Pteronisculus*.

Palaeopterygians (*sensu* Regan 1923) have received considerably less attention than the neopterygians; especially teleostean and their direct ancestors (Arratia 2004). Consequently, their evolutionary history and biology are poorly resolved (Lund *et al.* 1995, Dietze 2001, Lund & Poplin 2002; Cloutier & Arratia 2004). Palaeoniscoids and other basal actinopterygians were common in Asian freshwater bodies during the Triassic (Chang & Miao 2004). However, few Jurassic freshwater deposits host representatives of this group. Jurassic freshwater palaeoniscoids inherited a generalized anatomy from their Triassic and late Palaeozoic ancestors. In a sense they were ‘living fossils’ or relictual taxa by the mid-Mesozoic. Palaeoniscoids persisted in low diversity into the Early Cretaceous (Schultze 1970, Su 1985, Poplin & Su 1992), at which time most fish faunas were already dominated by advanced archaeomae- nids and teleostean (Chang & Jin 1996, Chang & Miao 2004). However, the modern teleostean fauna was still absent from some Early Cretaceous assemblages in China (Su 1985). Coccolipids ranged from the earliest Jurassic to the late Early Cretaceous (Hilton *et al.* 2004); this family is often considered to represent the last of the palaeoniscoids. They acquired rounded scales independently from other palaeopterygians, Amiidae and teleostean. During the Mesozoic, they spread almost worldwide and colonized both marine and freshwater environments. Coccolipids have been found on all continents except Africa and Antarctica. Although most coccolipids were small fishes, a few reached 45 cm long (Liu 1957).

In 2006, an expedition to the Aulie locality (Fig. 1), above the village of Kasharata [formerly Mikhailovka (Hecker 1948)] was organized by the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, and the K.I. Satpaev Institute of Geological Sciences, Almaty (Dzik *et al.* 2010). Nearly 400 well-preserved articulated palaeonisciform specimens were collected and are the basis for this study. Restoration of the skeletal anatomy of both palaeonisciform species from Karatau is presented here, together with a discussion of their possible relationships and the palaeobiogeography of the youngest palaeonisciforms.

**Geological setting**

The Karabastau Formation is exposed at several localities (Hecker 1948) in the Great Karatau, part of the Tian-Shan Mountains in southern Kazakhstan, Central Asia (Fig. 1) and the most common macrofossils are fish (Dzik *et al.* 2010). All the fossil material collected in 2006 and described in this paper comes from the Jurassic Karabastau Formation at the classic locality Aulie (Fig. 1, coordinates 42°53′50″N, 70°0′6″E). The approximately 10-m thick fossil-fish-bearing claystones exposed in the Aulie outcrop are composed of distinct dark (organic-rich) and light (dolomitic) laminae (Dzik *et al.* 2010). A large collection of plant, insect and fish remains were gathered during only one season of excavation at this Konservat-Lagerstätte (Grimaldi & Engel 2005). The age of the Karabastau Formation is difficult to determine due to its continental setting (Dzik *et al.* 2010, Doludenko & Orlovskaya 1976). Studies of plant macrofossils and palynomorphs have favoured age estimates of Middle or Late Jurassic (Dzik *et al.* 2010). The age of the Karabastau Formation is difficult to determine due to its continental setting (Dzik *et al.* 2010, Doludenko & Orlovskaya 1976). Studies of plant macrofossils and palynomorphs have favoured age estimates of Middle or Late Jurassic (Dzik *et al.* 2010) and these have been supported by international correlation of the insect faunas (Dzik *et al.* 2010).
Material and methods

New articulated specimens of two Jurassic palaeonisciform taxa from the Aulie locality are the main subjects of this study. One hundred specimens of *Pteroniscus turkestanensis* and 246 specimens of *Morrowellus aniscowitchi* were collected during one field trip (for the full list of specimens see Systematic palaeontology). Previously described and undescribed actinopterygian material from the Middle or Late Jurassic Karabastau Formation, held in several institutions listed below was also studied. Some representatives of the Coccolepididae were also studied for comparison. Specimens from the Karabastau Formation are housed at various museums. In 1977, Dr. Rosanoff gave four fish specimens from Karatau to MNHN, Paris (see the list of specimens below). Seven specimens were brought to NHMUK, London, by Professor Cockerell in 1928 and were described by White (1934). Four palaeonisciform specimens from the Jurassic of Karatau are also housed at the SMNS, Stuttgart. The type material studied by Gorizdro-Kulczycka (1926) is stored in the Museum of Geology, University of Tashkent.

Some of the Aulie specimens required mechanical preparation, which was carried out with a fine needle. Attempts to make transfers of the specimens attached to epoxy resin cover failed because the rock matrix resisted chemical preparation in formic acid. Some of the specimens were coated with Ammonium Chloride or immersed in glycerol before photography. Fish otoliths resist compaction and are visible under the dermal bone cover in many specimens. A thin black, but non-carbonaceous (as revealed by EDS: energy-dispersive-X-ray spectroscopic analysis) coating commonly defines the large orbit. Drawings were made using a binocular light microscope with a camera lucida attachment. SEM images were taken at the Institute of Paleobiology PAS, Warsaw, and in the Laboratory of Electron Microscopy and Microanalysis at the Institute of Geology of the Jagiellonian University, Cracow. Energy-dispersive-X-ray spectroscopic analysis EDS analysis was performed at the Institute of Paleobiology PAS, Warsaw. The photograph of specimen NHMUK PV P6302 was taken by the Photo Unit at the NHMUK, London.

**Terminology**

Anatomical terminology used for the axial skeleton and fins follows that of Mabee (1988) and Mabee et al. (2002). The terminology for scales and external morphology of the fins was recently summarized by Arratia (2009) and the terms used to describe advanced actinopterygians are applied here to basal actinopterygians. Dermal bone nomenclature follows Wiley (2008), Schultz (2008) and Poplin & Lund (1995).

**Abbreviations used in figures**

Abbreviations are as follows: al, anal fin lepidotrichia; ax, axonost (proximal row of dorsal fin supports); ba, bascots (distal row of dorsal fin supports); Ba, branchial arch part; Cl, cleithrum; cl, caudal fin lepidotrichia; Clv, clavicle; D, dentary; dcf, dorsal caudal fulcrum; Dh, dermohyal; dl, dorsal fin lepidotrichia; Dpt, dermopterotic; Dsp, dermosphenotic; ep, epural; Ex, extrascapular; f, fulcrum; ff, fulcra; hs, ganoid scale of upper caudal body lobe; ha, haemal arch; ha1–6, haemal arches supporting the ventral lobe of caudal fin; hyp, numerous shortened hypurals supporting the dorsal lobe of caudal fin; ioc, infraorbital canal of lateral sensory line; J, jugal; lls, lateral line scale; ID, left dentary; mdc, mandibular canal of lateral sensory line; mc, main lateral line canal; Mx, maxilla; N, nasal; na, neural arch; ndis, two reduced distal-most neural arches; Op, opercle; Pa, parietal; Pcl, postcleithrum; Pmx, premaxilla; poc, praopercular canal of lateral sensory line; Ppa, postparietal; Pop, praepercle; Psh, paraphrenoid; Pt, post-temporal; R, rostral; ra, radials supporting anal fin; Rbr, radii branchiostegii; Rd, right dentary; Sc1, supracleithrum; soc, supraocular canal of lateral sensory line; Sop, subopercle; Sr, scle- rotics; stc, supratemporal commissure; tc, tabular canal of lateral sensory line; vcf, ventral caudal fulcrum.

**Institutional abbreviations**

KG, ‘Karatau Gorizdro-Kulczycka’ collection in the Museum of Geology, Faculty of Geology, University of Tashkent, Uzbekistan; NHMUK, Natural History Museum, London, United Kingdom; MNHN, Museum national d’Histoire naturelle, Paris, France; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

**Systematic palaeontology**

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGII Cope, 1887
Order PALAEONISCIFORMES Goodrich, 1909
Family indet.

Remarks. *Pteroniscus* Berg, 1949 was assigned to the Palaeniscidae (Hecker 1948, Berg 1949), for which an original tentative diagnosis was given by Aldinger (1937) that was later emended by Nielsen (1942). Gardiner (1967) listed *Pteroniscus* within the Coccolepididae, but as no evidence was provided to support this decision, it is considered erroneous. In addition, Fowler (1971) listed *Pteroniscus* within the Thrissonotidae without providing any explanation. Su (1985) established a new family, Uighuroniscidae, to include the genera *Uighuroniscus*, *Indaginilepis* and possibly *Pteroniscus*. 
**Pteroniscus** Berg, 1949

1948 *Pteroniscus* Hecker, pp. 39, 40, fig. 16–23, pl. 11–13. pl. 15, fig. 2. (*nomen nudum*)


1964 *Pteroniscus* Berg, 1956 (*sic*); Berg, Kazantseva & Obruchev, p. 346, fig. 2. (*nomen nudum*)

Type and only species. *Oxygnathus turkestanensis* Gorizdro-Kulczycka, 1926.

**Emended diagnosis.** Palaeoniscoid fish with large preopercle with horizontal arm almost as broad as deep. Some pectoral lepidotricha serrated posteriorly. Number of lepidotrichia large, exceeding 20. Pelvic fin, dorsal fin and anal fin all broad based. Fulcal scales absent from base of pelvic fin; single fulcra present in front of anal fin; few fulcra in front of dorsal fin, and there are few ventral caudal fulcra. Scales along lateral line numerous (exceeding 50) up to the base of caudal fin; more than 10 scale rows above lateral line scale row below dorsal fin base, and similar or higher number of scale rows below lateral line scale row above pelvic fin base.

**Comments.** *Pteroniscus* was first mentioned by Hecker (1948) in a report on Karatau without any description of the fish, but authored by Berg and probably based on an unpublished manuscript of his. The original diagnosis of the genus was published later by Berg (1949).

**Pteroniscus turkestanensis** (Gorizdro-Kulczycka, 1926)

1926 *Oxygnathus turkestanensis* Gorizdro-Kulczycka, pp. 185–187, figs 1, 2.


Type specimen. A holotype was not designated by the original author of the species. The type collection studied by Gorizdro-Kulczycka (1926) was stored in the Main Central-Asian Museum (Glavnyi Sredne-Azatskii Muzei) in Tashkent. It is currently held in the Museum of Geology, Faculty of Geology, University of Tashkent, Tashkent. The only specimen of *Pteroniscus turkestanensis* identified so far among this collection is KG-1, which is here designated the lectotype.


**Locality.** Aulie, Great Karatau Range, Tian-shan Mountains, Kazakhstan.

**Formation and age.** Karabastau Formation, late Middle or early Late Jurassic.

**Diagnosis.** *Pteroniscus* with a lepidotrichial number close to 21 in the pectoral fin, 33 in the pelvic fin, 26 in the dorsal fin and 39 in the anal fin. Five to six fulcra in front of dorsal fin; four ventral caudal fulcra. Approximately 65 scales along lateral line, up to base of caudal fin; 11–13 scale rows above lateral line scale row below dorsal fin base and 12–16 scale rows below lateral line scale row above pelvic fin base.

![Fig 2. Part of the head of *Pteroniscus turkestanensis* (Gorizdro-Kulczycka, 1926); Specimen ZPAL V.32.10 preserved with ornamentation. Anterior part of the head is missing. A, Line drawing of the specimen; B, Photograph. Scale bars = 10 mm.](image-url)
Comments. Two species of palaeoniscoid fishes with ganoid scales, *Oxygnathus turkestanensis* and *Oxygnathus cf. ornatus* were recognized by Goridzro-Kulezycka (1926) in the material from the Karabastau Formation. Berg (1949) later assigned both to a single species within *Pteroniscus*.

Distribution. Besides those originating from exposures of the Karabastau Formation, one fish specimen from Lower Jurassic (Sinemurian) marine strata at Osteno, Italy, was listed as belonging to *Pteroniscus* (Pinna 1985), but neither a supporting description nor an illustration has been published.

Description

Only the external anatomy of *Pteroniscus* can be studied using the material from Karatau. The thick ganoid scale cover hides most of the visceral skeletal elements, except in two specimens in which dorsal and anal fin radials, supraneurals and impressions of neural and haemal arches can be observed where some scales are missing.

Skull ornamentation. The dermal cranium and shoulder girdle bones of *P. turkestanensis* are ornamented with minute tubercles and ridges (Fig. 2A–C).

Snout. Paired nasals and a single median rostral form the short, rounded snout. The anterior edges of both nasals and the median rostral are poorly preserved in all specimens, but the latter seems to be shorter than the nasals (Fig. 3D–G). The median rostral is somewhat rectangular and as broad as the nasal. In some specimens, the median rostral is split into a few minute, rounded to oval, irregularly edged bony plates (Fig. 3A–C). Some of these plates are perforated in the middle, which suggests a role as a sensory organ. Possibly, the snout of *Pteroniscus* carried accessory neuromasts or electoreceptors, but no similar structure has been observed in other palaeoniscoids. Highly distorted nasals are preserved lateral to the median rostral. They are L-shaped, lateral-line-bearing elements. The lateral line continues on to the parietal posteriad, but its anterior continuation cannot be traced due to the poor state of preservation of the tip of the snout. A rounded notch in the lateral margin of the nasal, which represents the posterior excurrent nostril, is visible only in three specimens. The anterior nasal opening is not visible.

Skull roof. Within the central series of the skull roof, the largest element is the rectangular parietal bone. It is twice as long as the nearly square postparietal.

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Fig 3. Peculiar inner structure of *Pteroniscus turkestanensis* rostral. A, Photograph of the head of specimen ZPAL V.32.752. Rostral marked with white box and enlarged in photograph C, and drawn (B). D, E, Drawings of rostral part as preserved in other specimens (ZPAL V32.37 and ZPAL V32.43+ respectively). F, G, Photographs of ZPAL V32.37 and V32.43+, respectively. Scale bar in A = 5 mm, in B, C = 1 mm.
The supraorbital lateral line canal runs along the lateral margin of the parietal and several short canals branch off along its length in the parietal. Anterior to the parietal, the supraorbital canal continues in the nasal and it enters the postparietal posteriad. The supraorbital canal disappears in the middle of the postparietal. The contact between parietals is clearly asymmetric in one specimen (ZPAL V.32.37), in which the suture is gently displaced towards the right bone. In other specimens, it seems to be strictly median and the line of contact between the two parietals is rather straight. A pineal (parietal) foramen is absent. The parietal sutures laterally with the dermosphenotic and dermopterotic. The long dermopterotic runs parallel to the skull roof bones and bears part of the temporal lateral line canal. Typically, the temporal lateral line is poorly preserved on the sides of the skull and only its posterior part is visible on the dermopterotic, from where it runs on to the extrascapular. The dermopterotic also sutures medially with the postparietal. Bones of the posterior skull roof series are poorly preserved, but enough is present to see that the occipital commissure runs transversely on the extrascapulars. The temporal canal extends in the post-temporal in the ventro-caudal direction to continue in the supracleithrum. The exact shape of the extrascapulars can not be traced in any of the specimens.

**Orbitals.** The margins of the orbit are clearly visible but bones delimiting it are typically distorted and it is difficult to trace the sutures between them. The nasal bone delimits the orbit anteriorly and, because of its poor state of preservation, it is unclear whether there is a further ossification forming the anterior orbit margin. Dorsally, the orbit is bordered by the dermosphenotic, and posteroventrally, by the jugal. The dermosphenotic tapers anteriorly and probably reaches the nasal at the line of suture between the nasal and parietal, or terminates close to it. The jugal bears a prominent infraorbital lateral sensory line with short branching posteriadal canals. The posterior margin of the jugal is poorly preserved, but the bone is somewhat crescentic. Very thin and delicate sclerotics are rarely preserved or in poor condition.

**Cheek.** The cheek bones are poorly preserved due to deformation resulting from the presence of otoliths. Only a few specimens (e.g., MNHN 1977_3.1) show preservation of a series of three small, somewhat rectangular, suborbitals. The preopercle is large and closely surrounds the dorsal and posterior edges of the maxilla. Its horizontal arm is triangular and almost as broad as deep; it is much larger than the vertical arm. The vertical arm is very narrow, but its exact shape can not be traced because it is poorly preserved. The preopercular canal runs along the posterior edge of the preopercle. The dermohyal is a small narrow triangular bone. It is rarely preserved (e.g., in ZPAL V.32.10) and, generally, its presence can be judged from the occurrence of a small space between the preopercle and opercle.

**Opercular region.** A wide oblique arch composed of the opercle and subopercle extends above the preopercle. The arch continues and curves downwards around the head in a series of branchiostegals. The first branchiostegal just below the subopercle is slightly larger than the lower ones, although it is recognizable only in five specimens (e.g., in ZPAL V.32.40). The exact number of branchiostegals is difficult to determine, but exceeds 12. The opercle is rectangular to oval and deeper than the subopercle. It is almost twice as deep as broad. The subopercle is nearly square to oval. Growth lines are visible on the opercle, subopercle and branchiostegals.

**Jaws.** A possible premaxilla was identified in one specimen (ZPAL V.32.749) due to its partially lateral and partially dorso-ventral compression. It is a very thin and small bone penetrated by a set of round holes, suggesting the presence of teeth. The maxilla is a very robust bone in its posterior part (behind the orbit) and it extends well backwards in the skull. It becomes very slender and curves gently upwards anteriorly (below the orbit). The ventral margin of the maxilla has a shallow depression in the middle, making it slightly S-shaped. The lower jaw is also a robust and long bone carrying the mandibular canal. Its posterior part is hidden under the maxilla in all specimens. An angular bone can not be identified in any of the studied specimens. The teeth, present on the maxilla and the mandible, are smooth, conical, numerous, of various sizes and irregularly distributed. They are present along nearly the whole length of the jaws and are present even on the edges of the posterior plate of the maxilla.

**Viscer al skeleton.** The hyomandibular bone is rather poorly preserved. It is long and broad, with an obtuse angle between the arms. The anterior margin of the horizontal arm seems to be the deepest part of the bone. It is not possible to determine its exact morphology.

**Parasphenoid.** Only the anterior part of this poorly preserved bone is visible. It is thin and bears small teeth on the midline ridge. It broadens posteriad, but the exact shape of this part can not be traced. Longitudinal growth lines are present along its anterior part in one specimen (ZPAL V.32.769).

**Inner ear.** A pair of large compaction-resistant otoliths is visible beneath the dermal bones of the cheek of the dorso-ventrally flattened specimens (ZPAL V.32.10, 37, 39, 114, 118, 770, 771). The cheek bones are frequently broken and a pale otolith is partially visible behind the orbit (Fig. 2A–B). It is deeper than broad, but no other details of its shape can be observed.

**Shoulder girdle.** The post-temporal is somewhat triangular with rounded posterior corners. In many cases, the post-temporal is poorly preserved and its anterior edge, where it sutures with the extrascapular, can not be traced. The contact between the post-temporal-
The supracleithrum is an elongate oval bone bearing the lateral line canal. Dorsally, the lateral line canal enters from the post-temporal and leaves posteriorly in the middle of the supracleithrum to continue on to the trunk. The cleithrum is a large bone covered anteriorly by the opercular arch and dorsally by the supracleithrum. The cleithrum is broadest in its upper part and gradually tapers and curves downwards. Its posterior edge is convex. In front of the pectoral fin base, the margin of a cleithrum shallows almost indistinguishably. The clavicle, rectangular to square, is present but covered by the branchiostegals and only its ventral edge is commonly visible. No trace of the cartilaginous elements of the girdle is preserved. A postcleithrum is absent.

**Lateral sensory line.** Canals of the lateral sensory line are visible on some of the dermal bones. Neither the most anterior parts of the supraorbital and temporal canals, nor the infraorbital canal are preserved in any of the specimens. Also, the mandibular canal is only partly preserved, without its posterior terminus. The straight preopercular canal is visible along the posterior edge of the preopercle. Its connections with other lateral line branches can not be traced. The parietal, extrascapular and jugal show canals that branch sparsely into prominent pore canaliculi. The pore canaliculi of the supraorbital and temporal are oriented laterally on the parietal. Branches can not be traced. The parietal, extrascapular and jugal show canals that branch sparsely into prominent pore canaliculi. The pore canaliculi of the supraorbital and temporal are oriented laterally on the parietal. They branch posterior from the infraorbital canal on the jugal and from the occipital commissure (= the supratemporal canal) on the extrascapular. Traces of the mandibular canal are barely evident as a series of a few round holes.

**Scales.** There are ca 65 scales along the lateral sensory line from the head to the base of the caudal fin; there are 11–13 scale rows below the base of the dorsal fin and above the lateral line (Berg 1949); there are 12–16 scale rows below the lateral line. The rhomboid ganoid scales (Fig. 4H) are arranged in vertical rows, passing from anterodorsad to posteroventrad, each trunk scale typically pegged in the one lying above via peg and socket articulation. Scale size and shape vary greatly on the entire trunk. The largest scales occur slightly above and below the lateral line.

The scales bearing the lateral line do not differ from others morphologically, except for having a ‘hump’ in the middle and an indentation in their posterior part. Scales of this region tend to be slightly deeper than broad.

The scales below the pectoral fins, between the lower parts of the left and right shoulder girdle, are highly variable in shape and size, being almost circular in outline. Their diameter decreases towards the ventral side of the head.

The scales above the bases of the pelvic and anal fins are also small. Those along the bases of the pelvic fins change in shape more significantly than those below the pectoral fins, but retain their connection with the vertical and horizontal rows of the trunk. Their depth decreases at least twofold, whereas their length remains stable. A similar change is evident above the base of the anal fin, although the difference is not so marked because the scales of the caudal peduncle are already smaller than those of the trunk.

All scales of the trunk and caudal peduncle are ornamented with several horizontal undulating ridges. The posterior margin of each scale has a few minute serrations projecting slightly to the posterior (Fig. 4H). The number of serrations per scale gradually decreases dorsad, ventrad and caudad, and ranges from around seven in the anterior portion of the trunk, to four on the caudal peduncle, and to two above the bases of the pelvic and anal fins.

The ornamentation on the scales and the serration of the posterior margins disappear around the region of the hinge line, which is not distinctly marked. As the scales of the caudal peduncle change their shape and gradually decrease in size towards the posterior, it is difficult to recognize the hinge line. Nevertheless, the scales behind the hinge line, up to the tip of the tail, clearly differ from others in being small, elongate, narrow and completely devoid of ornamentation as in other basal actinopterygians. The course of the lateral line in the upper caudal lobe is indeterminate.

The dorsal margin of the caudal fin is armed with a row of tightly arranged smooth fulcra. Three large elongate diagonal dorsal caudal fulcra extend anteriad to the caudal peduncle in front of the caudal fin (Fig. 4B). They are followed posteriorly by a series of more than two dorsal caudal fulcra, diminishing in size until they reach the tip of the fleshy caudal lobe. The fulcra extend slightly to the sides of the caudal fin and form a sharp ridge. Three fulcra border the ventral base of the caudal fin but, in many cases, they are poorly preserved (Fig. 4C). Five to six broad diagonal fulcra are present in front of the dorsal fin (Fig. 4D). Only one fulcrum borders the base of the anal fin (Fig. 4A). The fulcrum surface is ornamented with a few ridges parallel to its sides and meeting at the midline, except for the smooth examples covering the fleshy lobe of the tail. There are no fulcra in front of the base of the pelvic fin.

Fringing fulcra are visible only on the pectoral and caudal fins, although according to Berg (1949), they occur on all fins. Numerous small fringing fulcra are present along the anterior edge of the pectoral fin in only a few specimens (ZPAL V.32.766 and V.32.777). Fringing fulcra border the anterior margin of the ventral caudal lobe (Fig. 4E–F).

**Fins and fin supports.** All fins are segmented and composed of numerous lepidotrichia. Pelvic fins, anal fin and dorsal fin are all broad based. All fins have distally bifurcating lepidotrichia (except the few most anterior ones, which are noticeably shorter), although this is not evident in all specimens due to their poor preservation.
It is not determinable whether there is more than one bifurcation.

The pectoral fins originate within the ventral part of the flanks behind the shoulder girdle. Details of the support of the pectoral fin are not preserved. Pectoral fins are broad, trapeziform and reach a significant depth (comparable with the length of the maxilla). There are ca 21 lepidotrichia in the pectoral fin (19–25 according to Berg 1949). Two specimens have serrated posterior margins on the segments of the lepidotrichia. In one (ZPAL V.32.774), the pectoral fin is unnaturally stretched with the lepidotrichia spread apart. A minute sharp serration is visible under glycerol immersion, only on the upper part of the pectoral fin (Fig. 4G). It is not clear whether this is present on all lepidotrichia.

The pelvic fin lies medially on the body, it originates approximately at the middle of the trunk length. Its base is slightly shorter than the base of the anal fin. There are ca 33 lepidotrichia in the pelvic fin (approximately 40 according to Berg 1949). The pelvic fin is rhombic and nearly as deep as long.

The anal fin is the largest, nearly triangular, with an anterior margin four times deeper than the posterior one. It originates slightly posterior to the end of the dorsal fin. The total number of lepidotrichia is ca 39 (32–34 according to Berg 1949). A small part of the anal fin support is preserved in one specimen (ZPAL V.32.766). Seven slender radials with somewhat triangular distal ends are preserved in the middle of the fin (Fig. 5A–D).

The dorsal fin lies opposite the space between the pelvic and anal fins, and has a shape similar to that of the latter, but is markedly smaller. The number of lepidotrichia in the dorsal fin is ca 26 (22–24 according to Berg 1949). The dorsal fin support is partially visible in specimens ZPAL V.32.4+ and V.32.766 (Fig. 5A–B). About 13 radials supporting most of the base of the fin are preserved; their exact number is indeterminate. There are two rows of radials: baseosts and axonosts. The distal radials or baseosts are thick and short. The proximal radials or axonosts are only visible where their upper parts are close to the bases of baseosts. Axonosts are covered in their lower parts by scales and visible only as slender elevations. The baseosts are at least twice as long as the axonosts, but their exact shape is indeterminate.

The caudal fin is epicercal and not equilobate, with the upper lobe deeper and longer than the ventral lobe. Posterior margins of the dorsal and ventral lobes meet at the midline, forming a shallow near right-angle incision.
Basal actinopterygian affinity

Basal actinopterygian characters have been widely discussed in the literature (Moy-Thomas & Miles 1971, Schaeffer 1973, Patterson 1982, Gardiner & Schaeffer 1989, Lund & Poplin 1997). Some authors (Gardiner & Schaeffer 1989) further distinguished features of advanced basal actinopterygians in order to illustrate some morphological trends within the group. Attempts have been made to elucidate the systematic range of basal actinopterygians (Lund & Poplin 2002, Cloutier & Arratia 2004), but these rely on the few fossil taxa with modern descriptions available. *Pteroniscus* (Figs 6, 7) has a generalized basal actinopterygian anatomy in its many primitive characters: an oblique suspensorium, single median rostral, nasals bearing the supraorbital canal of the lateral sensory line, a crescentic dermosphenotic (possibly contacting or situated close to the nasal), a large anteriorly placed orbit, a large jugal carrying the infraorbital canal of the lateral sensory line, long jaws, a wide mouth gape, a maxilla with a deep postorbital part, a dermohyal present, a horizontal upper arm of the large preopercle, a branchiostegal number exceeding eight, basal fulcra present (except for the base of the pelvic fin), fringing fulcra present (at least on the pectoral and caudal fins), dorsal caudal fulcra, an epicercal tail with a prominent scaly dorsal body lobe and rhomboid ganoid scales with peg and socket articulation.

*Pteroniscus* also has a few advanced characters that separate it from the basal actinopterygian condition. These are the single dermopterotic bone in the temporal region and a parietal that is much longer than the postparietal. Also, the suborbitals are present. A postcleithrum, a feature of rather variable occurrence among basal actinopterygians, is absent in *Pteroniscus*. The poor preservation of specimens does not permit illustration of features of the neurocranium, premaxilla and axial skeleton.

Relationships of *Pteroniscus*

*Pteroniscus* Berg, 1949 was described as a member of Palaeoniscidae (Hecker 1948, Berg 1949, Berg et al. 1964). It is compared here with descriptions of the Late Permian *Palaeoniscum freieslebeni* Blainville, 1818, on which the family was established, and with other well-known representatives of this group: Early Triassic *Pteronisculus* (*Glaucolepis*) *stensioei* Nielsen, 1942; and the Late Triassic *Tursoedus acutus* Schaeffer, 1952 and *Tursoedus dolorensis* Schaeffer, 1967. The range of Palaeoniscidae was subsequently extended to the Early Cretaceous by several Asian forms assigned to this family: the Middle–Late Triassic *Ferganiscus osteolepis* Sytchevskaya & Yakovlev in Sytchevskaya 1999; Late Triassic *Triassodus yanchangensis* Su, 1984; Late Triassic *Shuniscus longianalis* Su, 1983; Early Jurassic...
**Weixiniscus microlepis** Su, 1994; Middle Jurassic *Palaeoniscinotus ningxiaensis* Su et al., 1997; and the Early Cretaceous *Cteniolepidotrichia turfanensis* Poplin & Su, 1992. The Middle Jurassic *Daqingshaniscus longiventralis* Chen, 1988, assigned to Palaeonisciformes, but to no particular family, is included here due to its supposed close relationship with *Pteroniscus* (Chen 1988). Both Early Cretaceous representatives of Uighuroniscidae, *Uighuroniscus sinkiangensis* Su, 1985 and *Indaginilepis rhombifera* Schultze, 1970, are possibly also closely related to *Pteroniscus* (Su 1985). *Indaginilepis* is the only non-Asian Cretaceous palaeoniscoid that bears similarities with *Pteroniscus* (Schultze 1970). All of the aforementioned species share some general morphological similarities (many have plesiomorphic characters) with *Pteroniscus* (Gorizdro-Kulczycka 1926). No phylogenetic analysis has included these forms. Therefore, it is not possible to place *Pteroniscus* within this group based on apomorphies (but see diagnosis).

A unique combination of morphological features variously distributed among the aforementioned taxa described in the literature is considered characteristic of *Pteroniscus*. Since the internal anatomy of this animal remains virtually unknown, the main diagnostic features are the dermal skeleton of the skull and shoulder girdle (Fig. 6), and the external morphology of the fins and body cover (Fig. 7). All compared taxa are taken into consideration with respect to their stratigraphic occurrence (Figs 8, 9). Features that are not preserved or poorly preserved are omitted. The comparisons below are based on bibliographic data as most of the comparative material was unavailable for the purpose of this study.

The Palaeoniscidae and Uighuroniscidae, plus *D. longiventralis* share numerous characters with *Pteroniscus*: (1) skull roof with the length of the parietal exceeding twice that of the postparietal — *P. ningxiaensis*, *D. longiventralis* and possibly *I. rhombifera* and *U. sinkiangensis*; (2) plain rectangular parietal without incision for the dermopterotic process — *F. osteolepis*, *T. acutus*, *T. dolorensis*, *P. ningxiaensis*, *D. longiventralis* and possibly *I. rhombifera* and *U. sinkiangensis*; (3) straight sutures between all skull roofing bones— *D. longiventralis*; (4) straight sutures at least between the parietal and postparietal— *F. osteolepis*, *T. acutus*, *T. dolorensis*, *P. ningxiaensis*, *I. rhombifera*, *U. sinkiangensis*; (5) paired extrascapulars— *F. osteolepis*, *P. ningxiaensis*, *U. sinkiangensis*; (6) lateral margins of the parietal suture anteriorly with the dermosphenotic and posteriorly with the dermopterotic — *F. osteolepis*, *D. longiventralis*; (7) orbitals (jugal...
and dermosphenotic) slender with narrow bones—*T. doloresis*, *T. yanchangensis*, *D. longiventralis*; (8) dermosphenotic tapers anteriorly and is close to or reaches the nasal with its anterior tip, no supraorbitals present—*P. stensioei*, *F. osteolepis*, *T. acutus*, *T. doloresis*, *D. longiventralis*; (9) three small rectangular suborbitals—possibly in *T. acutus*, *S. longianalis*, *U. sinkiangensis*; (10) opercle slightly deeper than the subopercle—*F. osteolepis*, *D. longiventralis*, *I. rhombifera*, *C. turfanensis*, *U. sinkiangensis*; (11) enlarged branchiostegal following the subopercle—*P. freieslebeni*, *F. osteolepis* and possibly *D. longiventralis*, *U. sinkiangensis*; (12) maxilla with deep rectangular posterior part close to the orbit and contacting the suborbitals only dorsally—*T. yanchangensis*, possibly *D. longiventralis*; (13) posteroventral corner of maxilla not prominent—*F. osteolepis*, *W. microlepis*, *P. ninxiaensis*, *D. longiventralis*, *U. sinkiangensis*; (14) S-shaped ventral margin of the maxilla (with shallow incision in the middle of its length and anterior part curved upwards)—*F. osteolepis*, possibly *S. longianalis*, *W. microlepis*, *C. turfanensis*; (15) anterior tip of the maxilla extends to the anterior edge of the orbit or slightly beyond it—*F. osteolepis*, *T. yanchangensis*, *S. longianalis*, *W. microlepis*, *P. ninxiaensis*, possibly *D. longiventralis*, *I. rhombifera*, *C. turfanensis*, *U. sinkiangensis*; (16) postcleithrum absent—*F. osteolepis*, *T. yanchangensis*, possibly *S. longianalis*, *W. microlepis*, *P. ninxiaensis*, *D. longiventralis*, *I. rhombifera*, *U. sinkiangensis*; (17) serration on posterior margins of lepidotrichial segments—*C. turfanensis*; (18) fulcra present in front of the dorsal and anal fins and in front of the caudal fin on the ventral side of the body—*P. freieslebeni*, *P. stensioei*, *T. acutus*, *S. longianalis*, *I. rhombifera*; (19) fringing fulcra present at least on one fin base—*P. freieslebeni*, *P. stensioei*, *F. osteolepis*, *T. acutus*, *T. doloresis*, *P. ninxiaensis*, *C. turfanensis*; (20) ventral, dorsal and anal fins similar in size and basal lengths—*D. longiventralis*, possibly *I. rhombifera*, *C. turfanensis*; (21) dorsal fin located opposite the gap between the ventral fin and origin of the anal fin—*F. osteolepis*, but with the anal fin moved far backwards, *D. longiventralis*, *I. rhombifera*, *C. turfanensis*, possibly *U. sinkiangensis*; (22) caudal fin inequilateral—*W. microlepis*, *P. ninxiaensis*, *D. longiventralis*, *I. rhombifera*, possibly *C. turfanensis*, *U. sinkiangensis*.

Each of these 22 detailed characters of *P. turkestanensis* is shared with at least one other species. One of the characters is common to nine other species (of the 13 taken into account). *Pteroniscus turkestanensis* is interpreted to be most closely related to the Middle Jurassic *D. longiventralis* (15 shared characters), Middle–Late Triassic *F. osteolepis* (13 shared characters) and Early Cretaceous *U. sinkiangensis* (12 shared characters). However, *P. turkestanensis* differs from all three species in having a larger pectoral fin and lacking an accessory opercle (present in *D. longiventralis* and *U. sinkiangensis*). Moreover, *P. turkestanensis* has a straight lower jaw and smaller and more numerous teeth than *F. osteolepis*. *Pteroniscus turkestanensis* has a
Fig 9. Palaeobiogeography of Coccolepididae, Palaeoniscidae, Uighuroniscidae, Daqingshaniscus longiventralis Chen, 1988 and Pteroniscus turkestanensis (Gorizdro-Kulczycka, 1926) during Jurassic (A) and Early Cretaceous (B). Shapes indicate locality age of Jurassic and Cretaceous respectively; circle—early epoch, squares—middle epoch, pentagon—middle or late epoch, triangles—late epoch of a period. 1, Morrison Formation, Morrolevpis schaefferi Kirkland, 1998; 2, Liassic of Lyme Regis, Coccolepis liassica Woodward, 1890; 3, Lower Parbeck, M. andrewsi (Woodward, 1891); 4, Solnhofen Limestone Formation, C. buckiard Agassiz, 1844; 5, Cheremkhovskaya Formation, Talepis rohoni Sytchevikaya & Yakovlev, 1985 and Palaeoniscinatus czemanovskii Rohon, 1890; 6, Karabastau Formation, Pteroniscus turkestanensis (Gorizdro-Kulczycka, 1926) and M. aniscowitchi (Gorizdro-Kulczycka, 1926); 7, Zhaogou Formation, Daqingshaniscus longiventralis Chen, 1988; 8, Yan’an Formation, Palaeoniscinatus ningxiensis Su et al., 1997; 9, Yumusha, Hengnan, Plesiococcolepis hunanensis Wang, 1977; 10, Xiangxi Formation, Weixiniscus microlepis Su, 1994; 11, Canadon Calcareo Formation, C. groeberi (Bordas, 1942); 12, Talbragar Fossil Fish Bed, C. australis Woodward, 1895; 13, Mons Basin, C. macroptera Traquair, 1911; 14, Wealden of Stadthagen, Indaginilepis rhombifera Schultze, 1970; 15, Shengjinkou Formation, Ctenolepidotrichia turfanensis Poplin & Su, 1992 and Uighuroniscus sinkiangensis Su, 1985; 16, Lower Huihuipoi Series, C. yumenensis (Liu, 1957); 17, Koonwarra Fish Bed, C. woodwardi Waldman, 1971. Pteroniscus occurrence reported from Italy, Osteno (Pinna, 1985) omitted. Middle Jurassic map is employed for the Jurassic. Numbers are not in a stratigraphic order. Map modified from Blakey (2008).
range of similarities with Early Cretaceous *I. rhombifera* (ten shared characters), Middle Jurassic *P. ninxiaensis* (nine shared characters) and Early Cretaceous *C. turfanensis* (eight shared characters), but it must be emphasized that due to the poor preservation of the specimens, only up to 14 of the various *Pteronis cus* characters could be compared with these species. Among this group, *C. turfanensis* shares a unique characteristic with *P. turkestanensis*: the serrated posterior margins of the lepidotrichial segments (Poplin & Su 1992). This character is less prominent in *P. turkestanensis* and is found only in the pectoral fin of a few specimens. In *C. turfanensis*, the serration is present on all preserved fins except the pectoral (Poplin & Su 1992). However, this feature is also found among other more distantly related actinopterygians [e.g., in ‘*Elonichthys*’ *hypsilepis* Hay, 1900 (Schultze & Bardack 1987, Poplin & Su 1992)]. Otherwise, *C. turfanensis* differs from *P. turkestanensis* in its dermal skull anatomy (especially in having a small orbit and curved jaws) and in the conspicuous ornamentation of its lower jaw (Poplin & Su 1992). Only a few common characters (up to five) are shared by *P. turkestanensis* and the other Asian palaeoniscids described above. However, this may be due to their poor preservational state. The earliest Palaeoniscidae have the least number of features in common with *P. turkestanensis*: only three characters in the Late Permian *P. freieslebenii* and the Early Triassic *P. stensioei*, five in the Late Triassic *T. acutus* and six in the Late Triassic *T. acutus*. All four of these species are well preserved and have been extensively described.

As there is no clear evidence demonstrating that *Pteronis cus* and *Palaeoniscum* are closely related, there is no reason to retain the previous family assignment. The observations reported above suggest a close relationship between *Pteronis cus* and *Daqingshaniscus*, which is currently not assigned to any family (Chen 1988). *Pteronis cus* also shows similarities to Asian *F. osteolepis* and *U. sinkiangensis*. Su (1985) proposed placement of *Pteronis cus* within Uighuroniscidae. However, the revision of *Pteronis cus* reveals more key differences from *Uighuroniscus* than previously recognized: fringing fulca in *Pteronis cus*, a small dermoteric not reaching the parial bone in *Uighuroniscus*, and the presence of a supraorbital bone separating the dermosphenotic from the nasal in *Uighuroniscus*. Most of the characters used to describe Uighuroniscidae by Su (1985) are currently considered to be generalized plesiomorphic features. Therefore, without current revision of *Uighuroniscus*, it is impossible to place *Pteronis cus* within this family. *Pteronis cus* also shares some common characters with other Asian palaeoniscids: *P. ninxiaensis* and *C. turfanensis*. This suggests that their assignment to the Palaeoniscidae is open to question. It should be stressed that because of the small number of characters available due to the specimens’ poor preservational state, the relationships discussed above can be further improved with new discoveries and further studies.

Family COCCOLEPIDIDAE Berg, 1940

1940 Coccolepididae Berg, p. 172.
1949 Coccolepididae Berg (sic); Berg, p. 466.
1964 Coccolepididae Berg, 1940; Berg et al., pp. 357, 358.


Emended diagnosis. Palaeoniscoid fish having rounded overlapping scales of the amioid type *sensu* Schultze 1996, mostly devoid of ganoin, or ganoin present as a very thin layer; a primitive skull with jaws extending posterior to the orbit; a robust maxilla occupying a large part of the cheek region, and with a very oblique suspensorium; robust jaws almost as long as head; dermosphenotic lacking contact or with only limited contact with nasal; a postcleithrum present; single series of radials supporting the dorsal fin; fulca may be absent; surface of dermal bones, scales and lepidotrichia either smooth or denticulate.

Comment on previous diagnoses. The single series of radials supporting the dorsal fin (Berg, 1940) is shared by all coccolepidids but is also represented in fish as remotely related as the Devonian *Minnipiscis* (Gardiner 1984, Choo 2011) and it is possibly a plesiomorphic condition. However, it is not known from many other primitive actinopterygians and some have up to three rows (Nielsen 1949, Romano & Brinkmann 2009). Hilton et al. (2004) suggested that the second row of supporting radials appeared late in ontogeny. However, this can be rejected because two of the largest coccolepidids, *Coccolepis yumenensis* (Liu 1957, Ma 1993) and *Coccolepis macropera* (Traquair 1911), have a single series of radials supporting the dorsal fin. Most coccolepidids are of small mature size, not reaching 20 cm, but the two aforementioned species exceeding 20 cm are sufficiently large for all the key features of the skeleton to be well developed. Gardiner (1960) listed the characters commonly observed in coccolepidids, but some were later found to be of restricted distribution (e.g., some coccolepidids have reduced ornamentation of the dermal skull and scales). Having more lepidotrichia than supporting radials (Berg 1940) is a feature shared by all basal actinopterygians and this quantitative character is of little taxonomic value. In the large collection of *M. aniscowitchi*, individual specimens differ in the number of radials and lepidotrichia. It is difficult
to determine whether all such delicate structures are preserved (Hilton et al. 2004) and their number may be subject to within-species variability. Confounding the problem is a dearth of published data on the postcranial skeleton (including the dorsal fin supports) of the palaeoniscoids (Hilton et al. 2004). The internal skeleton is commonly hidden beneath the ganoid scale cover. Therefore, it is usually only possible to compare the number of lepidotrichia between various species.

**Distribution.** An emended list (from Hilton et al. 2004) of coccolepidid occurrences and type localities is given in Fig. 9.

**Morrolepis** Kirkland, 1998

**Type species.** *Morrolepis schaefferi* Kirkland, 1998,


**Emended diagnosis.** Coccolepidids with bones of dermal skull and lepidotrichia that lack denticles. Scales with a strongly reduced number of denticles. Heavy ganoid scales in the lateral line with a morphology different from amnioid scales sensu Schultz (1996) covering the rest of body. Lateral line scales thicker than flank scales and without parallel ridges on their covered surface. Lower jaw narrow, straight, with an acute anterior part.

**Comments.** The key characters that differentiate *M. schaefferi* from its older relative *M. aniscowitchi* are the more anterior location of the pelvic fins and their fusiform shape (Kirkland 1998). Two rows of abdominal haemal arch ossifications are present in *M. aniscowitchi*. The haemal elements are arranged in pairs attached to the notochord from below. In *M. schaefferi*, these two rows are interpreted as haemal arch remains and as accessory ‘basiventrals’ (Kirkland 1998). This aspect of the axial skeleton is not fully understood and its structure may have resulted from the fossilization process (e.g., by increasing the distance between elements). Therefore, it is excluded from the diagnosis. It should also be noted that the row of lateral line scales is doubled in many specimens of *M. aniscowitchi* as a result of distortion and compression of specimens, and something similar may have happened with the paired, but not fused, ossifications of the haemal arches, where both left and right elements are visible.

Berg (1948) synonymized *Palaeoniscoidus turkestanensis* Sewertzoff, 1934 with *Coccolepis aniscowitchi*, probably being influenced by the material presented by Sewertzoff (1934, fig. 15) in his diagrammatic drawing. Eremeeva (1940) published a paper with the same figures as Sewertzoff (1934), but her identification of the specimens was different from his. In Sewertzoff’s (1934) work, there is no diagnosis, description or explanation for erecting the genus, therefore, it is considered a **nomen dubium** here.

**Morrolepis aniscowitchi** (Gorizdro-Kulczycka, 1926)

1926 *Coccolepis aniscowitchi* Gorizdro-Kulczycka, pp. 187–189, fig. 3.
1926 *Coccolepis socialis* Gorizdro-Kulczycka, pp. 189, 190, fig. 4. (**subjective synonym**)
1934 *Coccolepis cockerelli* White, pp. 396–399, fig. on p. 397. (**subjective synonym**)
1934 *Palaeoniscoidus turkestanensis* Sewertzoff, pp. 433–435. (**nomen dubium**)
1940 *Coccolepis aniscowitchi* Eremeeva, pp. 324–327, figs 1–5.
1940 *Coccolepis* n. sp. (sic) Eremeeva, pp. 327–332, 336, figs 6–7, 10, 15, 16. (**subjective synonym**)
1940 *Coccolepis martynovi* Berg; Eremeeva, pp. 333–336, figs 11–13. (**subjective synonym**)
1948 *Palaeoniscoidus turkestanensis* Sewertzoff, 1934 synonym of *C. aniscowitchi*; Berg, p. 1243. (**nomen dubium**)
1949 *C. martynovi* Berg; Berg, pp. 468, 469. (**subjective synonym**)

**Misspellings:** *C. aniskowitchi*, *C. aniskowitschi*, *C. anitschk*, *C. turkestanicus* [all in Sewertzoff (1934)], *C. socialer* (Liu 1957).

**Type specimen.** A holotype was not designated for *C. aniscowitchi* by the original author. The type collection studied by Gorizdro-Kulczycka (1926) was stored in the Main Central-Asian Museum (Glavnyi Sredne-Aziatskyi Muzei) in Tashkent and is currently deposited in the Museum of Geology, Faculty of Geology, University of Tashkent, Tashkent. The collection includes four specimens attributable to this species: KG-2, KG-3, KG-4, KG-5, of which the most complete specimen, KG-3, is here designated the lectotype. The holotype of the synonymous *Coccolepis cockerelli* White, 1934 (NHMUK PV P14528) is deposited in the Natural History Museum in London.

**Referred material.** *Morrolepis aniscowitchi* (Gorizdro-Kulczycka, 1926) (Coccolepis cockerelli White, 1934): NHMUK PV P14528, P16379–P16383.


**Comparative material.** *Morrolepis andrewsi* (Woodward, 1891): NHMUK PV P6302.
Coccolepis liassica Woodward, 1890: NHMUK PV P887, P894, P3694, P4370a, P6153, P11772, NHMUK PV OR39865.

Locality. Aulie, Great Karatau Range, Tien-Shan Mountains, Kazakhstan.

Formation and age. Karabastau Formation, late Middle or early Late Jurassic.


Comments. Eremeyeva (1940) identified elements of the pelvic girdle proximal to the radials in three species: C. aniscowitchi, C. martynovi and her ‘Coccolepis sp. nov’. Berg (1940, 1948) reviewed a large collection of coccolipeds from several localities in the Great Karatau Range and summed up his work by stating that the species recognized previously by Gorizdro-Kulczycka (1926), Sewertzoff (1934) and White (1934) are indistinguishable from each other and should all be treated as synonyms, together with Coccolepis sp. nov. of Eremeyeva (1940). Berg (1948) designated C. aniscowitchi Gorizdro-Kulczycka, 1926 as the valid name of this species. Coccolepis socialis and C. cockerelli represent juveniles of C. aniscowitchi. Coccolepis martynovi Berg, 1940 was proposed as a separate species characterized by its large adult size (Berg 1949, Eremeyeva 1940). None of the specimens examined in the present study can be compared with the material of Eremeyeva (1940) since the crucial structures of the pelvic girdle are not visible. Whatever the actual status of C. martynovi and C. cockerelli, there is no evidence that more than one species of Morrolepis is represented in the material from the Aulie locality forming the basis of the present study.

Description

Skull ornamentation. The dermal cranium and shoulder girdle of M. aniscowitchi is devoid of ornamentation typical of many basal actinopterygians. Only a few bones show traces of minute ornamentation.

Snout. The rostral region is heavily damaged in all specimens. It is a rather delicate and inconspicuous narrow part of the skull. The nasals are narrow and bear the supraorbital lateral sensory line. The nasal openings are indeterminate. The median rostral is poorly preserved in dorso-ventrally compressed specimens and is not evident in laterally compressed specimens. This is a rather narrow bone and its exact morphology remains unknown. Presumably, a premaxilla is present below the nasal, being a roughly T-shaped bone bearing holes and projections. The visible holes and projections may be broken teeth or they could be ornamentation (Fig. 10A–B, E–F).

Skull roof. The largest bone of the central series is the parietal, which is three times longer than the postparietal. The suture between the parietals is straight. The pineal foramen is absent in all specimens. The posterior part of the parietal is markedly broader than the anterior two-thirds of this bone. The anterior medial corner of the parietal extends down towards the snout region. Anteriorly, it sutures with the rostral and nasal; laterally, with the dermosphenotic and dermopterotic; and posteriorly, with the postparietal. Minute rounded tubercles are visible on part of the parietal in one specimen (ZPAL V.32.870). A prominent lateral sensory line canal runs along the lateral margin of the parietal. Anteriorly, the supraoccipital canal continues on to the nasal bones and posteriorly on to the postparietal. It curves towards the midline and disappears in the centre of the postparietal. The square postparietal is of equal width to the parietal and has a somewhat rounded posterior part. The medium-sized dermopterotic is somewhat triangular, with an anterior margin deeper than the posterior one. A minute but wide extrascapula is present and bears the supratemporal commissure of the lateral sensory line. The extrascapula is poorly preserved (Fig. 10A–F).

Orbitals. It is difficult to trace the pattern of bones surrounding the orbit (Fig. 10A–F). The anterior margin of the orbit is bordered by the nasal. The narrow crescentic dermosphenotic forms its upper margin. The dermosphenotic tapers anteriorly and contacts the nasal with its anterior tip. The posterior edge of the dermosphenotic is poorly preserved as are the lower and posterior parts of the orbit. Slender pieces of sclerotics are visible.

Cheek. The postorbital region is never preserved due to its compression over the otolith (Fig. 10A–F). Judging from the orbit size and the shape of the maxilla and opercular bones, the cheek region was rather small in M. aniscowitchi. Invariably, the preopercle is poorly preserved, but seems to be a narrow bone. A preopercular sensory canal runs close to its posterior margin. The exact margins of the preopercle are indeterminate. However, the position of the horizontal arm of the preopercle is delimitated by the space left the between the opercular arch and the maxilla (Fig. 10A–D). The exact shape and size of the dermohyal can not be determined.

Opercular region. Both the opercle and subopercle are rectangular. They are equally broad, but the latter is not as deep. The opercular arch is oblique, with the subopercle extending posteriorly beyond the hind skull roof (Fig. 10A–F). Approximately 12 branchiostegal rays are preserved only below the lower jaw and do not reach the subopercle in any of the specimens. In the space...
between the jaw and the subopercle, a large portion of cleithrum is usually the only visible element. The anteriormost branchiostegal is slightly wider and shorter than the others.

**Jaws.** The length of the jaws equals the length of the skull roof. Jaws extend far back behind the orbit. The maxilla has a deep posterior part with a posterodorsal corner projecting downward (Fig. 10A–B). The ventral margin of the maxilla is covered with teeth along its entire length. The anterior part of the maxilla is very slender and tapers anteriorly. The lower jaw is narrow and straight, with an acute anterior part. Its posterior edge is covered by the maxilla. The ventral part of the lower jaw thickens into a longitudinal bulge, which may be the mandibular lateral line canal. No trace of an angular is visible in the lower jaw. The jaws bear irregularly spaced small, smooth conical teeth, many of which are minute.

**Visceral skeleton.** Only fragments of the visceral skeleton can be observed in the material. Evidence of
the hyomandibula is rarely preserved. It is curved, rather narrow and long. Remnants of the branchial arches are visible in some specimens beneath crushed dermal bones. They are preserved as fragmentary thick rods obliquely oriented and parallel to the opercular arch (Fig. 10B–C).

Parasphenoid. Only the anterior part of this bone is preserved. The parasphenoid extends along the orbit and is very slender (Fig. 10E–F).

Inner ear. A pair of large otoliths is commonly preserved behind the orbit. The otoliths are ovoid with a slightly narrower ventral side. They are deeper than broad. Their exact morphology is unknown because of the overlying dermal bones.

Shoulder girdle. The triangular post-temporal borders the hinge of the skull roof. Anteriorly, it sutures with the extrascapula, and it is unclear whether there is any contact between the post-temporals. The post-temporal bears part of the main lateral sensory line canal (Fig. 10C–D). The main lateral canal continues on to the poorly preserved narrow supracleithrum and further on to the trunk (Fig. 10E–F). The supracleithrum may be ornamented with slender and short ridges, which run parallel to the anterior margin of the bone. Below the supracleithrum, a slender arched cleithrum is partially visible. It is mostly covered by the post-temporal, supracleithrum, opercle and subopercle. A rounded postcleithrum is situated behind the cleithrum and above the point of origin of the pectoral fin (Fig. 10A–D). The clavicle is not preserved in any of the specimens. Cartilaginous elements of the shoulder girdle are also absent.

Lateral sensory line. Only portions of the sensory canals are preserved. The parietal and nasal bones bear a robust supraorbital canal with only a few small canals branching off laterally above the orbit. The supraorbital canal runs down the nasals to half of the orbit depth, where it is too poorly preserved to be traced. The preopercular canal is visible on the preopercle. The postotic (temporal) canal, the supratemporal commissure and the main canal join on the small extrascapula. Only a short length of the postotic canal runs on to the dermopterotic and then it is too poorly preserved to be traced. A longitudinal bulge along the lower jaw is tentatively identified as the mandibular canal. There is no trace of the infraorbital canal.

Scales. The scales are thin, rounded and overlapping (Fig. 11A). They are of similar size along the whole trunk. Their surface is covered with ridges that converge slightly at a point in the posterior part of the scale (Fig. 11D). This feature is characteristic of amioid scales sensu Schultze (1996) and distinguishes them from cycloid scales of advanced actinopterygians, which have concentric ridges parallel to the margin of the scale (Schultze, 1996). The scales of the ‘softer’ regions close to the belly show more diagenetic alteration. Deformation of the scales (formation of a ‘bump’ in the middle) indicate that they were very thin and flexible, with their anterior part possibly somewhat thicker. Each scale is deformed in a specific way by the progressive post-mortem collapse of the body. The posterior margin of the scale appears more susceptible to deformation, presumably because it was thinner. Scanning electron micrographs reveal that the surface of the scales is smooth, and tiny triangular projections appear only on their posterior margin (Fig. 11B). These projections are more numerous on the lateral sensory line scales, forming a serration at their posterior edge. The lateral sensory line scales are more robust than the other trunk scales (Fig. 11E). They differ from other scales in being covered by a shiny layer of ganoin and lacking the ridges characteristic of amioid scales sensu Schultze (1996). Each of the scales has a distinct anterior and posterior part separated by a narrow depression. In the anterior part, there are two small lateral knobs and two larger knobs in the middle, all oriented longitudinally. The posterior region is thicker than the anterior part. It bears minute ridges and a serrated posterior edge. The opening for the canal of the lateral sensory line is not recognizable within these solid scales. It is not clear, therefore, whether the robust lateral sensory line scales bear the lateral sensory line canal itself or just follow the course of the lateral sensory line along the trunk. The lateral line ends with a few flat and rectangular scales that run from the body axis to the ventral margin of the dorsal fleshy lobe along the base of the tail fin. No trace of the lateral sensory line canal is visible in the upper caudal lobe.

Approximately 70 scales form the lateral line scale row. The entire scale cover is never preserved completely; therefore, exact counts of the scale number are impossible. Minute and slender diagonal ganoid scales cover only the upper lobe of the tail. Their length exceeds their depth and they diminish in size towards the tip of the tail. The hinge line is marked between the thin and rounded scales covering the trunk and the rhomboid scales on the caudal fleshy lobe. Rhomboid scales covering the caudal lobe are like those in all other basal actinopterygians. Transverse rows of those scales consist of five to six scales. A series of roughly 40 dorsal caudal fulcra covers the upper edge of the tail starting from its base above the first epural. One enlarged scale may be present at the anterior base of the anal fin in a few specimens. There are no fulcra bordering any other fin base.

Fins and fin supports. All fins have distally bifurcated and numerous segmented lepidotrichia. The lepidotrichia may bifurcate at least three times, although this is commonly hard to trace. Lepidotrichia have smooth surfaces (Fig. 11F). Pelvic, dorsal and anal fins are broad based. A few anteriormost lepidotrichia in these fins are shorter and not bifurcated.
The slender fan-shaped pectoral fins originate on the ventral side of the flanks. The number of lepidotrichia in the pectoral fin varies from 21 to 26. The dorsal edge of the fin is bounded by a thickened lepidotrichium. The support of the pectoral fin consists of a few radials (in most specimens four, although there may be one or two more radials) that are short and tightly arranged. The lowermost radial is the largest and is commonly the only skeletal element visible, whilst the remaining elements are hidden beneath it. The distal ends of the radials are slightly broadened. Supporting radials are preserved at a marked distance from the cleithrum, Fig 11. Scale and lepidotrichium morphology of Morrolepis aniscowitchi (ZPAL V.32.892). A, Overlapping scales of amioid type with denticles on posterior margin; A’, Restoration of the scales body covering; B, Detail of posterior margin of body covering scale showing denticle protruding posteriorly; C, Example of post mortem deformations of the trunk scales, scales from part of the trunk close to ventral; mean protuberance in the center of scale visible; D, Detail of the posterior of body covering scale showing the center of radiation of ridges; E, Lateral line scales; E’, Restoration of the scale from lateral line; F, Smooth surface of lepidotrichia without trace of ornamentation. Scale bars in A = 200 μm, in B = 20 μm, in C = 200 μm, in D = 50 μm, in E = 1 mm, in F = 400 μm.
which suggests the presence of a small lobe at the base of the pectoral fin.

Pelvic fins originate anterior to the middle of the trunk. They have ca 40 lepidotrichia. They are somewhat rhombic, with the anterior edge being more than two times longer than the posterior edge.

The anal fin originates posterior to the end of the dorsal fin. It has ca 33 lepidotrichia. The base of the

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**Fig 12.** Posterior portion of axial skeleton and caudal fin supports of Morrolepis aniscowitchi and M. andrewsi; A and C, M. aniscowitchi ZPAL V.32.691+, B and D, M. andrewsi NHMUK PV P6302 (photo courtesy Natural History Museum, London). Median fins are shaded light grey for ease of viewing. Scale bar = 5 mm.
anal fin is slightly shorter than those of the pelvic and dorsal fins. It is triangular with its anterior edge more than three times longer than the posterior one.

The triangular dorsal fin is located in front of the anal fin. It originates slightly posterior of the beginning of the pelvic fin. The dorsal fin has ca 40 lepidotrichia. The anterior margin of the dorsal fin is five times longer than the posterior margin.

The dorsal, anal and pelvic fins are supported by similar fin supports (one row for each fin). All are supported by a roughly equal number of radials. Each radial has a broadened distal end, and in the most completely preserved dorsal and anal radials, distinctly and deeply forked proximal bases are evident (Fig. 12A, C). Radials supporting the pelvic fins are the shortest among all fin supports. The length of the radials supporting the anal fin is intermediate between those supporting the pelvic and dorsal lepidotrichia. Radials supporting the dorsal fin decrease markedly in size from anterior to posterior, with the last radial three to four times shorter than the first.

The caudal fin is epicercal and inequilobate. The dorsal and ventral lobes are markedly separated along the body axis, with a deep and sharp incision. Both lobes of the tail fin are equal at their maximum depth. The caudal fin is supported by a modified distal part of the axial skeleton described below. The number of lepidotrichia is difficult to estimate.

Axial skeleton. Neural and haemal arches are present along the entire length of the trunk (Fig. 13B). In the abdominal part, each neural arch consists of two small parallel rods arranged in pairs so that each left and right rod are joined in their central part. Below the dorsal fin, the neural arches become more slender and elongate, with neural spines oriented posteriad, and they have markedly broadened bases. The neural arches attain their maximum length along the anterior part of the caudal peduncle and decrease in size towards the base of the caudal fin. The last three neural arches are bent strongly posteriad and they disappear below the row of epurals. Haemal arches are present in the abdominal part as small ossifications set in pairs. Below the posterior part of the dorsal fin, the shape of the haemal arches becomes similar to the shape of the neural arches. Their bases are broad and triangular, and their spines may be

![Fig 13. Morsolepis aniscowitchi (Gorizdro-Kulczycka, 1926), late Middle or early Late Jurassic Karabastau Formation, Aulie, Kazakhstan. A, Reconstruction of the body and B, Axial skeleton and fin supports, C–D, Specimen ZPAL V.32.691 and its counterpart with both scales and axial skeleton visible. Scale bar = 10 mm.]
longer than those of the neural arches. The haemal spines shorten gradually towards the base of the caudal fin. Six posterior spines are elongate and are set at a lower angle to the body axis. These six distinct haemal arches form a support for the ventral lobe. Shortened hypurals are present further posteriorly. The hypurals reduce their length caudad and form a very dense and strong skeletal support for the dorsal lobe of the tail (Figs 12A, C, 13B). The exact number of elements supporting the dorsal lobe is unknown due to their small size and tight arrangement. Moreover, they are covered by ganoid scales on the caudal fin. The supraneurals (exceeding 16) are very slender elements that continue to the upper caudal lobe. Their exact number is unknown, but at least 11 hypurals are present below the thick cover of the dorsal caudal fulcra. The ventral bases of the epurals are broad. The first one or two proximal epurals are located above the last, almost spineless, neural arch. The notochord is not enclosed dorsally by any osseous element in the posterior part of the caudal peduncle. A row of slender supraneurals is present in the anterior abdominal region. The supraneurals (exceeding 16) run above the neural arches from the head to the dorsal fin, where they disappear, giving way to the radials supporting the dorsal fin. In the posterior part of the caudal peduncle, a row of epurals runs above and behind the last of the neural arches. The epurals are slender elements that continue to the upper caudal lobe. Their exact number is unknown, but at least 11 epurals are present below the thick cover of the dorsal caudal fulcra. The ventral bases of the epurals are broad. The first one or two proximal epurals are located above the last, almost spineless, neural arch. The notochord is not enclosed dorsally by any osseous element in the posterior part of the caudal peduncle.

**Basal actinopterygian affinity**

*Morrolepis aniscowitchi* (Figs 13, 14) displays the following set of basal actinopterygians characters (Schaeffer 1973, Patterson 1982, Gardiner & Schaeffer 1989): rod-shaped branchials, an oblique suspensorium, a single median rostral, nasals bearing the supraorbital canal, a crescentic dermosphenotic in contact with the nasal, a large anteriorly placed orbit, long jaws, a wide mouth gape, a maxilla with a deep postorbital part, a horizontal upper arm of the large preopercle, numerous branchiostegals, a persistent notochord, dorsal caudal fulcra, straight supraneurals extending from the skull to the base of the dorsal fin, lepidotrichia exceeding the number of supporting radials, an epicentral tail with a prominent scaly dorsal body lobe, the distalmost haemal spines modified into hypurals, paired neural spines not merged, and numerous rod-shaped epurals. The advanced characters of *M. aniscowitchi* include having a single dermopterotic bone in the temporal region, the presence of a postcleithrum and a parietal much longer than the postparietal. This species also shows some unique characters derived from the basal actinopterygian condition described below. Several important features are indeterminate because some key parts of the material are not preserved. Among the features that are impossible to trace are the neurocranium, dermohyal, suborbitals, gular and clavicle, the detailed morphology of the premaxilla, the rostral and bones delimiting the orbit.

*Morrolepis aniscowitchi* is derived from a basal actinopterygian condition having reduced basal fulcra (except for the possible presence of anal fulcra), with fringing fulcra absent and amnion scales sensu Schultze (1996).

**Osteological comparison within the Coccolepididae**

A thorough review of the literature on coccolepidids was made by Hilton *et al.* (2004). Unfortunately, some earlier descriptions of these fishes lack details of their morphology, and no distinction between apomorphic and plesiomorphic characters was made. Coccolepidids have slender bodies and most are small fishes that do not exceed 20 cm. Ornamentation of the dermal skull and shoulder girdle with tubercles and ridges is generally reduced on the bones of the coccolepidids except for British Early Jurassic *Coccolepis lissica* Woodward, 1890 (Gardiner 1960) and South American Late Jurassic *Coccolepis groeberi* (Cione & Pereira 1987). Bone ornamentation is limited to particular bones in a few species: the parietal and supracleithrum in *M. aniscowitchi* redescribed here and the nasal in European Late Jurassic *Coccolepis bucklandi* (Hilton *et al.* 2004) and Australian Early Cretaceous *Coccolepis woodwardi* (Waldman, 1971). Large coccolepidid parritals usually exceed the postparietals in length by at least three times, but can be even four or five times longer in the largest species *Coccolepis yumenensis* from the Early Cretaceous of Asia (Liu 1957, Ma 1993). The suture between the parritals is straight in three species (*M. aniscowitchi, C. bucklandi, C. yumenensis*), although there may be some variation of this species.
state in the Asian Early Jurassic *Plesiococcolepis hunanensis* (Wang 1977) and *C. woodwardi*. The post-parietal of coccolepidids is squared with a generally straight suture separating this pair of bones. *Coccolepis yumenensis* is an exception in having a sinuous suture between the postparietals, and postparietals with antero-medially projecting corners. The extrascapulas in all known forms are small bones either paired and contacting along the midline (*M. aniscowitchi*, *C. bucklandi* and probably also *C. woodwardi*) or four in number and set in a row (*P. hunanensis*, *C. yumenensis*). The dermopterotic is a medium-sized bone of variable shape (from a somewhat elongate oval in *P. hunanensis* to more triangular in *M. aniscowitchi* and *C. bucklandi*), but otherwise poorly characterized in this family.

*Plesiococcolepis hunanensis* and probably also *Coccolepis macroptera* (Traquair, 1911) from the Early Cretaceous of Europe differ from other coccolepidids with a rounded snout in having a prominent rostral part. Little is known about this delicate region of the coccolepidid skull, except that the nasals seem to be generally narrow and the median rostral broad. It is also difficult to trace the premaxilla in the coccolepidid snout. The bone is possibly present only in *P. hunanensis*, *M. aniscowitchi* and *C. woodwardi*. The last two have a similar, roughly T-shaped, bone closing anteriorly the snout [called the ‘rostropremaxilla’ by *C. woodwardi* (Waldman 1971)]. It bears many minute teeth or projections and a few larger ones. They are preserved as small openings, retaining broken projections in some cases. Whether these are true teeth or projections similar to those known in the redfieldiids can not be ascertained (Poplin & Lund 1995).

The orbit is surrounded by the nasal, small antorbital (present at least in *C. liassica*, *P. hunanensis*, *C. yumenensis* and *C. woodwardi*), jugal and dermophenotic (although these are rarely preserved). The crescentic dermophenotic has only limited contact with the nasal on its anterior tip in *M. aniscowitchi* and is probably separated from the nasal in other species. A supraorbital, separating the nasal from the dermospheotic (close to the centre of the trunk), dorsal position and its depth does not exceed the maximum depth of the maxilla. A slight exception is *P. hunanensis*, where the horizontal arm of the preopercle shows a limited increase in size towards the anterior and its depth does not exceed the maximum depth of the maxilla. The horizontal arm of the narrow coccolepidid preopercle shows a limited increase in size in most coccolepidids (*P. liassica*, *P. hunanensis*, *M. aniscowitchi*, *C. bucklandi* and *C. yumenensis*). Two to three suborbitals are visible in *C. liassica*, *P. hunanensis*, *C. bucklandi* and *C. yumenensis*. The horizontal arm of the narrow coccolepidid preopercle shows a limited increase in size towards the anterior and its depth does not exceed the maximum depth of the maxilla. A slight exception is *P. hunanensis*, where the horizontal arm of the preopercle is triangular and at least as deep as the maxilla. *Plesiococcolepis hunanensis* is also unique in lacking a dermohyal. The morphology of the opercular arch in coccolepidids varies: the opercle can be deeper than the subopercle (*P. hunanensis*, *M. aniscowitchi*, *C. bucklandi* and possibly *C. groberi*) or vice versa (*C. liassica*, *C. yumenensis* and *C. woodwardi*).

Most coccolepidids have long jaws that are equal in length to the skull roof (measured from the tip of the parietal to the end of the post-temporal). A generalized primitive palaeoniscoid maxilla with a deep rectangular posterior part is present in *C. liassica* and *C. woodwardi*. The antero-dorsal margin of the maxilla seems to be more skewed, giving the impression of gradual tapering of the maxilla in the rostral direction, in *P. hunanensis*, *M. aniscowitchi*, *M. schaefferi* and *C. groberi*. Most coccolepidids have teeth of two sizes: regularly spaced large ones with numerous smaller ones between them. However, *C. bucklandi* has only one row of teeth on the lower jaw, and *M. aniscowitchi* has teeth that vary less in size and are irregularly distributed.

Coccolepidids have a rather uniform shoulder girdle, with a triangular post-temporal and elongated supracleithrum extending to the centre of the subopercle depth (except *C. bucklandi*), and the cleithrum followed by a round postcleithrum (not present in *C. bucklandi*). About five radials supporting pectoral lepidotrichia are evident only in *M. aniscowitchi* and *C. yumenensis*. They broaden distally with the ventral radial being the largest. A thickened lepidotrichium forms the dorsal edge of the pectoral fin in these species. The dorsal margin of the pectoral fin is bordered by fringing fulcra in *C. bucklandi* and possibly also in *C. yumenensis*. The distribution of this character among other members of Coccolepididae has not been determined.

The median fins of the coccolepidids are broad-based, in most cases triangular, similar in size and each is supported by one row of radials. They differ slightly in their location in relation to the trunk and other fins. In most coccolepidids (*C. liassica*, *P. hunanensis*, *M. aniscowitchi*, *M. schaefferi*, *C. yumenensis*, possibly *M. andrewsi*, *C. groberi* and *C. macroptera*), the median fins originate in the following order: pelvic fins (close to the centre of the trunk), dorsal fin (above or posterior to the pelvic fin) and anal fin (below or posterior to the dorsal fin). Exceptionally, the dorsal fin is positioned more anteriorly and originates in front of or at the same position as the pelvic fin in *C. bucklandi* and *C. woodwardi*. In all known cases, the median fin-supporting radials are rod-like ossifications with broadened distal ends (also described as ‘forked’ bases, e.g., in *P. hunanensis*, *C. yumenensis* and *M. schaefferi*). Both broad and ‘forked’ ends are visible in *M. aniscowitchi*; the broadened ends are in fact forked distal endings of the radial. The identification of this feature probably depends on the degree of ossification and preservation. It is worth noting that radials in *M. aniscowitchi* are also distinctly divided at their proximal bases, but they are not broadened (Fig. 12A, C). The length of the fin-supporting radials may vary. For example, in *M. aniscowitchi*, the radials supporting the pelvic fin are the shortest of all fin-supporting radials, whereas all such radials are of similar length in *C. yumenensis*. Moreover, the supporting radials may be of equal size in one fin, but gradually decrease in size.
towards the posterior in another (as in the dorsal fin of *M. aniscowitchi*).

Two of the earliest known coccolepidids (*C. liassica* and *P. hunanensis*) are unique in having a pelvic bony plate additionally supporting the pelvic fin. This is larger in *Plesiococcolepis*, where it is situated along the base of the pelvic fin (Wang 1977). There is no trace of such a plate in the examined collection of *M. aniscowitchi*, despite being mentioned in earlier works (Sewertzoff 1934, Eremeyeva 1940; see also comments on diagnosis). *Morrolepis* is derived in having a reduced number of fulcra or lacking them in front of the median fins.

The epicentral caudal fin of coccolepidids is generally unequilobate and deeply cleft. Two exceptions are: *C. yumenensis*, where it is nearly unequilobate, and *C. groeberti*, which has a fully unequilobate tail.

A persistent notochord is sheltered by similar skeletal elements in all members of the family. Three regions can be readily distinguished: the anterior abdominal (in front of the dorsal fin), the median (from below the dorsal fin to the end of the caudal peduncle) and the posterior region (at the base of the caudal fin). The abdominal region is characterized by small rod-like paired neural arches and usually minute, somewhat oval, paired haemal arch elements. The region is distinct in the presence of slender supraneurals that exceed the short neural arches in length. The supraneurals disappear at the origin of the dorsal fin. The last two supraneurals are clearly inserted below the first supporting radials of the dorsal fin in *M. aniscowitchi*, *M. schaefferi* and *C. bucklandi*. In the median region, both paired neural and haemal elements are made more distinct by having broadened triangular arches and elongate spines. The haemal spines are longer than the neural spines in the caudal peduncle. The last two neural arches have shortened neural spines, which are somewhat bent caudally in *M. aniscowitchi* and *M. andrewsi* (Fig. 12). The neural arches disappear in front of the base of the tail, leaving the posterior part of the notochord unprotected on its dorsal side. A row of thin rod-like epurals is present in the posterior region and continues in the dorsal caudal lobe. The exact number of epurals is not known because they are covered by the dorsal fulcra in all species. The first two epurals are situated above the last neural arch in *M. aniscowitchi* and *M. andrewsi* (Fig. 12). Haemal spines are elongate in the caudal peduncle and become even longer, thicker and more tightly arranged at the base of the caudal fin. One exception is *C. bucklandi*, in which these spines remain relatively short and are not closely packed. The modified distal parts of terminal haemal spines form the caudal fin support. The ventral lobe is supported by six haemal arches (located below the midline). The dorsal lobe is supported by an indeterminate number of noticeably shorter epurals that decrease in size towards the tip of the dorsal fleshy lobe. They are covered by ganoid scales and can not be described in detail.

The unique and most distinctive characters of coccolepidid scales are the rounded scales of amioid type. In the type species, *C. bucklandi*, these scales bear numerous tiny denticles, whereas in other species (*C. liassica*, *C. australis* and *C. woodwardi*) they bear tubercles that are easy to recognize by light microscopy. *Morrolepis andrewsi* has been reported (Woodward, 1895) to have tubercles covering only the scales of the abdominal region (although not preserved in specimen NHMUK PV P6302). *Morrolepis aniscowitchi* has denticles restricted to the posterior margin of the scales and *M. schaefferi* has completely smooth scales (Kirkland 1998). Preservation of the delicate scales of *M. aniscowitchi* varies, depending mainly on their location on the trunk. Post-mortem processes resulting in the formation of a ‘bump’ (see above) in the middle of some of the scales, caused some misunderstanding in the original description of *M. aniscowitchi*, with Gorizdro-Kulczycka (1926) referring to a single large protuberance in the middle of each scale (Fig. 11C). Agassiz (1843) first mentioned the occurrence of ganoin tubercles in *Coccolepis*, and their presence was confirmed by Hilton et al. (2004). SEM analysis revealed that the scales of *M. aniscowitchi* are smooth with sparse denticles restricted to their posterior margin (Fig. 11A, B).

Robust lateral line scales (Fig. 11E), which also have a serrated posterior margin, at least in *M. aniscowitchi*, do not resemble the amioid scales sensu Schultz 1996 covering the body and are unique to *Morrolepis*. The presence of robust lateral line scales along the midline of *M. andrewsi* (Fig. 12B, D), which has not been reported previously, and the absence of evident tubercles on the scales covering most of the body, allows tentative assignment of this species to *Morrolepis*. The only specimen (NHMUK PV P6302) examined in the present study lacks the anterior part of the body and, therefore, all details of the skull. The well-preserved axial skeleton is similar to the skeleton known from *M. aniscowitchi* (Fig. 12A, C).

The overall similarity of coccolepidid species results from the retention of many plesiomorphic characters of their palaeoniscoid ancestors. However, there are some differences in the distribution of the plesiomorphic characters, e.g., the presence of a set of basal fulcra in some younger species. Coccolepidid scales share a few apomorphies that make them distinct from basal actinopterygians, e.g., amioid scales (Schultz 1996), or a single row of unfused supporting radials in the dorsal fin. The postcranial internal skeleton of extinct Actinopterygii is still not completely understood (Arratia 2008). It is sporadically preserved in some palaeoniscoids [e.g., in Devonian *Mimpiscis* (Choo 2011) and Triassic *Pteronisculus* (Nielsen 1942)] despite their massive cover of ganoid scales, and in few cases when ganoid scale cover is somehow reduced, as in *Phanerosteon, Birgeria* (Nielsen 1949), saurichthyids and coccolepidids. Despite the fact that coccolepidid fossils vary greatly in their state of preservation and are mostly
incomplete, a comparison between them reveals a conservative plan of their postcranial anatomy. Although not known in many other fossil actinopterygians, this may be of diagnostic value.

Evolution of the Coccolepididae

The two oldest Early Jurassic coccolepids, the marine Coccolepis liassica from Lyme Regis, Great Britain (which may actually not belong to Coccolepis; Schultzze, pers. comm. 2013) and the freshwater Plesiococcolepis hunanensis from Hengnan, China, differ from younger forms in having pelvic bones, which were probably lost subsequently. The presence of pelvic bones was also reported for the coccolepid specimens from Karatau (Sewertzoff 1934, Eremeyeva 1940) not examined in this study, but this has not been confirmed in the material from Aulie. Possibly, another coccolepid species retaining a pelvic girdle occurs in the Great Karatau or perhaps Morrolepis aniscowitchi developed this feature at a late ontogenetic stage that is not represented in the material examined in the present study.

The most probable scenario for the evolution of coccolepids is that all the younger Asian coccolepids are descendants of the European marine Coccolepis (probably close to C. liassica) and that the distinct Asian Plesiococcolepis lineage has vanished from the fossil record before younger coccolepids entered Asia. Coccolepis australis is known from Late Jurassic of Australia (Turner et al. 2009). Coccolepis survived in the freshwaters of Australia until the Early Cretaceous, and C. australis may be a direct ancestor of C. woodwardi from the Aptian Koonwarra site, Australia. Another Coccolepis is known from Late Jurassic of South American freshwater deposits. It is probable that relatives of both C. australis and South American C. groeberi differentiated in the Late Jurassic and expanded their range to at least Australia and South America. The genealogy of the Asian, Early Cretaceous C. yumenensis from the freshwater Lower Huihuipou Series is unresolved. It is similar in age to the European freshwater C. macroptera from the Mons Basin. Coccolepis yumenensis inhabited a lake that presumably contained salt water (Ma 1993) and it is, therefore, probable that it reached Asian waters via a marine route. Morrolepis schaefferi from the Kimeridgian Morrison Formation, North America, being only slightly younger than M. aniscowitchi, is its closest relative. The Middle Jurassic Asian freshwater coccolepid Yalepis rohoni (Sytechevskaia & Yakovlev 1985, Sytechevskaia 2006) seems to be phylogenetically distant from all other coccolepids and is only tentatively assigned to this family.

Conclusions

A detailed osteological study revealed extensive new information on the anatomy of two palaeoniscoids from the Jurassic of Karatau. In the light of these new data, Pteronisculus Berg, 1949 can no longer be considered a palaeoniscid. Revision of its assumed relationship with Middle Jurassic Asian Daqingshaniscus Chen, 1988 and Early Cretaceous Eurasian Uighuronicidae supports previous suggestions (Su 1985, Chen 1988) that all of those fishes are distinct from the Palaeoniscidae. Their morphological resemblance to several Asian forms: Middle–Late Triassic Ferganiscus Sytechevskaia & Yakovlev in Sytechevskaia, 1999 and probably also to the Early Cretaceous Cteniolepidotrichia Poplin & Su, 1992 and Middle Jurassic Palaeoniscinotus ningxiensis Su et al., 1997 emphasizes the need for revision of the Palaeoniscidae. Pteronisculus turkestanensis (Gorizdro-Kulczycka, 1926), compared here with all Asian Mesozoic palaeoniscoids of supposedly close morphological similarity and age, remains within an unresolved evolutionary relationship at family level.

Thorough descriptions of Indaginilepis Schultzze, 1970 from the Early Cretaceous of Europe and Cteniolepidotrichia (Poplin & Su 1992) and the present revision of Pteronisculus highlight the fact that palaeoniscoids—usually considered generalized basal actinopterygians—are poorly understood. Further detailed study may reveal disparity within this group that could lead to the resolution of their evolutionary relationships.

Morrolepis aniscowitchi (Gorizdro-Kulczycka, 1926) is one of a few palaeoniscoids with an exceptionally preserved axial skeleton. Here, features of the distal part of the axial skeleton are considered to be diagnostic. Two coccolepid species consistently possess six haemal arches supporting the lower part of the caudal fin, and two shortened distalmost neural arches. These characters are stable within the studied specimens of M. aniscowitchi and are both present in the only studied specimen of M. andrewsi.

Morrolepis aniscowitchi, together with two other Late Jurassic species [M. schaefferi Kirkland, 1998 and M. andrewsi (Woodward, 1891)] comprise a close monophyletic group within Coccolepididae, with M. aniscowitchi being possibly the oldest known representative of this genus [depending on the exact age of the Karabastau Formation, which is difficult to estimate and has been approximated to Middle–Late Jurassic (Doludenko & Orlovskaya 1976, Dzik et al. 2010)]. Despite the earliest fossil record of Morrolepis in the Middle or Late Jurassic, the unique character of thickened scales in the lateral line covered with shiny layers of ganoin suggests that it retained more primitive characters than other coccolepids, which have thin scales that are devoid of ganoin cover.

The persistence of basal actinopterygians in Asian freshwaters of the Mesozoic (Chang & Miao 2004) is well exemplified by the Karatau locality, where this group outnumbers other actinopterygians (Hecker 1948), even though the diversity of advanced and primitive palaeoniscoid species is similar. Similar
disproportion can be traced back at least to the Triassic in North China, where basal actinopterygians were the main component of freshwater faunas, whereas more advanced fishes dominated in the marine environment (Jin 2006).

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