# THE ANATOMY, AFFINITY AND PHYLOGENETIC SIGNIFICANCE OF *ILEMORASPIS KIRKINSKAYAE* (OSTEOSTRACI) FROM THE DEVONIAN OF SIBERIA

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ABSTRACT—*Ilemoraspis kirkinskayae* is a poorly known genus of Osteostraci (stem-gnathostome) yet is one of the most distinct in terms of its anatomy and biogeography. It is paleobiogeographically isolated from all but one other genus of Osteostraci on the Altaid microcontinents and is one of the few genera to survive into the Middle Devonian. Discovery of a new locality in Khakassia, Russia, has yielded a number of exceptionally well-preserved specimens of the genus and subsequently a wealth of new anatomical information. A new reconstruction of *Ilemoraspis* is provided, including post-cranial anatomy and a sensory line extending onto the trunk. The latter is a novel observation for the Osteostraci and allows the proposal of a scenario for the evolution of trunk lateral lines. New anatomical data for *I. kirkinskayae* allow testing of established hypotheses on its affinity. Our analyses yield two equally parsimonious solutions that appear unlikely on the basis of comparative anatomy or paleobiogeographic grounds, respectively. This situation is likely to be a consequence of the sporadic sampling of osteostracans in central Asia.

## INTRODUCTION

Evidence supporting the placement of Osteostraci as the sister taxon of gnathostomes has grown in recent years (Forey and Janvier, 1993, 1994; Forey, 1995; Donoghue et al., 2000; Donoghue and Smith, 2001) and as such, they are integral to understanding one of the most importance episodes in vertebrate evolution-the establishment of the gnathostome bodyplan. Despite the importance of the Osteostraci, a phylogeny for the clade has not been established, scenarios of paleobiogeographic evolution are incomplete and the anatomy and taxonomy of many of its constituent taxa need further investigation (Janvier and Newman, 2005; Sansom, 2007). Key to resolving these problems are the Siberian genera (Tannuaspis, Tuvaspis and Ilemoraspis) due to their paleobiogeographic isolation as well as their unique and poorly characterized anatomies. The discovery of a new locality yielding many well-preserved specimens of Ilemoraspis in Khakassia, South Siberia, enables us to do so.

The Osteostraci are known from deposits across the Northern hemisphere but during Siluro-Devonian times, they were distributed across two continents—Laurussia (also known as Euramerica) and Siberia. The osteostracan fauna of these continents has been used to define two main faunal provinces—the cephalaspid province of Laurussia and the tannuaspid province of the Altai-Sayan area, Siberia (Young, 1981, 1990; Blieck and Janvier, 1991). Laurussia was formed by the fusion of Baltica, Avalonia, and Laurentia in the Silurian (Scotese and McKerrow, 1990; Cocks and Torsvik, 2005) and was home to the majority of osteostracan diversity. The paleogeographic history of the Siberian terrane and associated Peri-Siberian terranes is complex; a much more limited osteostracan fauna is known from the Tuva-

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Mongol terrane (including modern day Tuva) and the West Sayan terrane unit (including modern day Khakassia). These microcontinents were just north (present day south) of the continent of Siberia (Şengör et al., 1993; Cocks and Torsvik, 2002, 2007; Yolkin et al., 2003). During the Early Paleozoic, these micro-continents formed island arcs that became accreted to the Siberian continent (Bachtadse et al., 2000; Cocks and Torsvik, 2007). Given this geological history, the tannuaspid fauna would have been isolated from all other Osteostraci, thus raising questions about distribution, survival, ecology, and anatomy of the Siberian taxa. Unfortunately, we currently have a very incomplete picture due the paucity and quality of specimens as well as imperfect knowledge of the geological setting.

Tannuaspis levenkoi Obruchev, 1956, and Tuvaspis margaritae Obruchev, 1956, are from Late Silurian and Early Devonian deposits of the Republic of Tuva, Russia. They are known from only two macro-specimens and scattered scales. The specimens enable a reconstruction of an osteostracan with tremataspidoidlike morphology and galeaspid-like ornamentation of pointed, costulate tubercles (Afanassieva and Janvier, 1985:figs. 2, 3). *Ilemoraspis kirkinskayae* Obruchev, 1961, from the Republic of Khakassia, was known from a single distorted specimen allowing only a rough reconstruction (Afanassieva and Janvier, 1985; Blieck and Janvier, 1999) of an osteostracan quite unlike any other (Fig. 1). It possesses large unfused tesserae and small lateral and median fields but the condition for even the most basic of diagnostic features, such as cornua or paired fins, was difficult to establish.

A new locality for *Ilemoraspis* in North Khakassia was discovered by a field team of Tomsk State University, led by S. Rodygin in the summer of 2004. This and subsequent return visits have yielded a number of extremely well-preserved specimens. These specimens allow a complete reconstruction and description of *Ilemoraspis kirkinskayae*. Its age, geographical isolation and



FIGURE 1. The holotype of *Ilemoraspis kirkinskayae* Obruchev, 1961, PIN 1642/1. **A**, PIN 1642/1 from Obruchev (1964:pl. 2, fig. 1); **B**, Interpretation of the holotype from Afanassieva and Janvier (1985:fig. 5B); **C**, Reconstruction of Afanassieva and Janvier (1985:fig. 6). Scale bar equals 1 cm.

anatomy make it highly unusual amongst the Osteostraci and, therefore this new reconstruction enables a much more complete picture of osteostracan evolution.

Institutional Abbreviations—PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; PM TGU, Paleontological Museum, Tomsk State University, Russia.

## GEOLOGICAL SETTING

The Republic of Khakassia is located in Asiatic Russia, south of the Krasnoyarsk region, north of the Mongolian border (Fig. 2). Devonian outcrops are known from the Minusinsk depression. The type locality for *Ilemoraspis kirkinskayae* mentioned by Obruchev (1961) is in the area of Chazy-Koyza, approximately 50 km west of Abakan (Fig. 2) and belongs to the Ilemorovskaya Formation. The Ilemorovskaya Formation is dated as late Givetian by reason of its plant remains (Melestshenko et al., 1973; Afanassieva and Janvier, 1985; Parnachev, 1998; Afanassieva, 2004). The newly discovered locality is 2 km southwest of Shira, northern Khakassia (Fig. 2). The locality is situated in a layer of interbedded sandstones and siltstones (aleurolites), predominately of a fine-grain size. The fossiliferous layer is 4.9 m in thickness and occurs 2 m above the base of the interbedded

sandstones and siltstones. The tuffaceous sandstones of the fossiliferous layer are pink-yellow, greenish-brown in color and contains quartz, various plagioclases and siliceous rocks. Tuffaceous siltstones lie above and below the sandstone bed.

Stratigraphically these rocks belong to the middle member of the Pridorozhnaya body. This body is approximately equivalent to the upper Matarakskaya body of the Shunet Mountain section, part of the Matarakskaya Formation. The Pridorozhnaya is assigned to the Lower Devonian by reason of the fossil land plants (rhyniophytes) known from localities throughout. Within the Pridorozhnaya, *Margophyton goldschmidtii* Halle, 1916 (Zakharova, 1981), and *Drepanophycus gaspianus* (Kräusel and Weyland, 1948) are found in association with *Ilemoraspis*, restricting its age from late Pragian to middle Emsian (Ananiev et al., 1972; Gensel, 1992; Parnachev, 1998). Also found in the Pridorozhnaya (although not at the *Ilemoraspis* locality) are unidentified conchostracans and eurypterids. The continental deposits are of lacustrine origin, the salinity of which is unknown.

The region during the Early Devonian is characterized by volcanic activity as evidenced by beds and lenses of basalt, trachyteandesite and trachyte-rhyolite-dacite. Volcanic activity was at a low level during the formation of the Pridorozhnaya, but was much higher below (lower Matarakskaya Formation) and above (lower Shunetskaya Formation). In the absence of Eifelian sediments for the region, the Emsian is uncomformably overlain by the Givetian beds, during which a shallow-marine sea invaded the area (the Tashtyp transgression).

## SYSTEMATIC PALEONTOLOGY

Class OSTEOSTRACI Lankester, 1868 Subclass CORNUATA Janvier, 1985c Order indet. Subfamily TANNUASPIDINAE? Obruchev, 1964 (sensu Sansom, in press) Genus *ILEMORASPIS* Obruchev, 1961

**Type Species**—*Ilemoraspis kirkinskayae* Obruchev, 1961. **Diagnosis**—As for type and only species.

## ILEMORASPIS KIRKINSKAYAE Obruchev, 1961 (Figs. 3-6)

Ilemoraspis kirkinskayae Obruchev, 1961:561.

Ilemoraspis kirkinskayae Obruchev: Obruchev, 1964:132, pl. 2, fig. 1.

Ilemoraspis kirkinskayae Obruchev: Afanassieva and Janvier, 1985:501, figs. 5, 6.

Ilemoraspis kirkinskayae Obruchev: Afanassieva, 1991:106.

Ilemoraspis kirkinskayae Obruchev: Afanassieva, 2004:259, pl.15, figs. 3-5.

**Holotype**—PIN 1642/1, incomplete and distorted dorsal headshield.

**Type Locality and Horizon**—Chazy-Koyza, Southern Minusinsk basin, Khakassia, Russia; Ilemorovskaya Formation, Middle/Late Givetian, Middle Devonian.

**Referred Material, Locality, and Horizon**—PM TGU 1028-3-1/130, posterior trunk segment; 1028-3-2/130, dorsal right side of headshield; 2017-20/130, 2017-21/130, part and counter-part of caudal fin; 2017-22/130, 2017-23/130, 3007/130, posterodorsal section of head shields with cornua; 2017-24/130, headshield with dorsal and ventral elements; 2017-25/130, headshield with ventral elements and complete cornua; 3001/130, 3002/130, 3003/130, and 3005/130, assorted articulated body sections. All are from the Pridorozhnaya body, Matarakskaya Formation (lower Emsian), 2 km southwest of Shira, Khakassia, Russia.

**Revised Diagnosis**—Medium-sized osteostracan with headshield just longer than wide (6–7 cm length, 5–6 cm wide); ros-





trum round; cornua long, thin; cephalic shield with paired anteromedial grooves on dorsal surface anterior to orbits; orbits widely spaced (interorbital distance four times orbit width); nasohypophysial division round; lateral fields small, oval, with slight median indentation; cephalic dermoskeleton consisting of large unfused tesserae ornamented with fine sinuous ridges.

### DESCRIPTION

The new material enables a more complete understanding of the anatomy of Ilemoraspis kirkinskayae. Previous reconstructions of the head shield (Fig. 1C; Afanassieva and Janvier, 1985) have an incorrect shape due to the severe distortion and incomplete nature of the holotype. PM TGU 1028-3-2/130 (Fig. 3) and F3 PM TGU 2017-25/130 (Fig. 4A) demonstrate a longer headshield F4 (approximately 80% of shield width). Furthermore, I. kirkinskayae clearly possesses cornua at the posterolateral corners of the head shield (Fig. 4A, B), a key diagnostic feature within Osteostraci. The cornuae are freestanding, separated from the body by the pectoral sinus. As previously established, there is a very short abdominal division. The abdominal division shows no trace of fused lateral scales such as those seen in certain Thyestiida (Sansom, in press). The body and the cephalic shield are therefore distinct in terms of scales and ornamentation. The orbits are very widely spaced (interorbital distance at least four times the orbit width). The pineal opening, normally located at the midpoint of the orbits is not immediately apparent. There is no independent pineal plate. The holotype possesses a small area with a change in ornamentation on the median tessera just anterior to the median field, between the orbits, potentially indicating a pineal opening (Afanassieva and Janvier, 1985). Apart from the holotype, this tessera is preserved only in PM TGU 1028-3-2/130 where it is slightly distorted and there is no change in ornamentation. The median field is long (width is 40 per cent of shield length) with a straight posterior margin. The openings of the endolymphatic ducts are observed in PM TGU 1028-3-2/130 (Fig. 3B) and PM TGU 2017-22/130 located external to the median field laterally, in the groove between two tesserae. The lateral fields are short and wide (width 40 per cent of length). The lateral fields have a median indentation giving a 'kidney' shape.

The nasohypophysial opening (Fig. 3B) is located in the midline, uncommonly far forward from the pineal opening (twothirds of the pineal-endolymphatic duct distance). The nasohypophysial opening, like that of Tannuaspis, is round. A pair of anteroposteriorly directed dorsal grooves (Fig. 3B, 4B, 5B) are F5 located lateral to the nasohypophysial opening and anterior to the orbit. These 'grooves' are interpreted as an apomorphy of Ilemoraspis kirkinskayae. The hypothesis of Afanassieva and Janvier (1985), that the groove is a distinct anatomical feature rather than a gap between tesserae or a supplementary sensory line, is confirmed by the PM TGU specimens (1028-3-2/130, 2017-24/130 and 2017-2/130). The groove originates close to the orbit and terminates close to the cephalic margin. It possesses a rounded and deep margin, which has the same ornamentation as the dorsal surface. There are symmetrical ventral impressions of the grooves on PM TGU 2017-25/130 (Fig. 4A, B) upon the cast of the oralobranchial chamber, potentially indicating that the slits could have acted as a passage connecting the oralobranchial chamber and the dorsal surface. Taking a section through such a groove however, (see histology below) indicates that there is a dermoskeletal floor to the groove and as such, it did not act as a passage. An alternative interpretation is that of a highly developed sensory groove but as PM TGU 1028-3-2 indicates (Fig. 3), the groove has a morphology distinct from that of the preserved and extensive sensory line system in terms of size, shape and direction. Interpretations of the function of the groove thus remain open.

JOURNAL OF VERTEBRATE PALEONTOLOGY, VOL. 28, NO. 3, 2008



FIGURE 3. *Ilemoraspis kirkinskayae* PM TGU 1028-3-2/130, cephalic shield in dorsal view. **Abbreviations: cm, cmm**, transverse sensory canals; **dgr**, dorsal groove; **end**, external opening of the endolymphatic duct; **fin**, pectoral fin; **ifc**, infraorbital sensory canal; **lf**, lateral field; **lc**, **lc2**, lateral sensory canals; **mf**, median field; **nh**, nasohypophysial opening; **orb**, orbit; **pls**, posterolateral scales. Scale bar equals 1 cm.

The dermoskeletal cephalic shield of I. kirkinskayae consists of large tesserae that are loosely attached to each other following preservation. The tesserae of the cephalic shield and scales of the body are ornamented with fine sinuous ridges (Fig. 5C, D), a feature appearing in widely disparate taxa, including certain tremataspidoids and others (Janvier and Newman, 2005; Sansom, in press). The ridges are broadly parallel and aligned with the margins of the cephalic shield and other anatomical features. The lateral and median fields differ in ornamentation, having much smaller tesserae (Fig. 5C). PM TGU 2017-24/130 and PM TGU 2017-25/130 show that the margin of the ventral surface of the shield consisted of the same large tesserae as dorsally whilst the covering of the oralobranchial chamber consisted of much smaller tesserae. PM TGU 2017-15/130 (Fig. 4A), presumably formed by sediment infilling the oralobranchial chamber, reveals the chamber's general circular shape. No gill external branchial openings or branchial arches are preserved.

Extensive sensory lines are observed on the cephalic shield. The infraorbital sensory line is directed anteroposteriorly, medial to the dorsal groove and lateral fields (Fig. 3). Furthermore, in addition to the usual transverse (cm, cmm) and lateral (lc) sensory line canals, there is another lateral sensory line, between the lateral margin of the shield and the lateral field (lc2). Furthermore, a lateral line canal (Fig. 4C, D) is observed extending along the lateral surface of the body, parallel to the ventral margin edge, a novel observation for the Osteostraci (see discussion below).

A reconstruction of the rest of the body of *I. kirkinskayae* is now possible from a number of extremely well-preserved specimens. Significantly, it is clear that *Ilemoraspis kirkinskayae* had paired pectoral fins (PM TGU 1028-3-2/130, PM TGU 2017-23/ 130, PM TGU 2017-25/130), unlike the tremataspidoids and *Tannuaspis*. The fins are broad and round, with small tesserae located anteriorly that grade into very small tesserae posteriorly (Fig. 3, 4A, B). The same condition is observed in the paired fins of most other Osteostraci.

The caudal region is also preserved. Whilst none of the preserved caudal regions are articulated with the diagnostic cephalic



FIGURE 4. *Ilemoraspis kirkinskayae*. **A**, **B**, infiling of oralobranchial chamber and ventral cephalic shield surface in dorsal view, PM TGU 2017-25/130 with stereograph pair (A) and interpretation (B), where grey is matrix; **C**, **D**, segment of trunk with lateral line, PM TGU 3002/130; **E**, **F**, caudal region demonstrating epicercal condition, PM TGU 2017-21/130. **Abbreviations: cor**, cornual process; **dgr**, dorsal groove; **dls**, dorsolateral scales; **fin**, pectoral fin; **lc** lateral sensory canal; **ls**, lateral scales; **mdrs**, median dorsal ridge scales; **ors**, scales or tesserae covering the ventral floor of the oralobranchial chamber; **vrs**, ventral ridge scales. Scale bar equals 0.5 cm for A and 1 cm for C and F.

←

shield, these specimens can be confidently assigned to *I. kirkinskayae* by reason of the typical fine sinuous ridge ornamentation. Furthermore, trunk scales articulated with the headshields are identical in morphology to those articulated with the trunk and



caudal regions. The tail (Fig. 4E, F) is clearly epicercal, with fin rays extending posteroventrally from the dorsally extended caudal axis. The dorsal and ventral lobes of the caudal fin are approximately equal in size. Most Osteostraci possess a horizontal caudal lobe, but there is no evidence of this feature in *I. kirkinskayae*. Furthermore, there is no anal fin, which is consistent with the condition observed in all other Osteostraci. Anterior to the caudal fin, small pointed median dorsal ridge scales (Fig. 4C–F) line the dorsal midline. The presence of anterior and posterior dorsal fins is not known, potentially due to the incomplete preservation of these regions. PM TGU 3002/130 indicates a potential absence of posterior dorsal fin, at least in a posterior position.

## HISTOLOGY OF ILEMORASPIS KIRKINSKAYAE

Almost all of the specimens exhibit mouldic preservation and fine details of the skeletal anatomy and ornamentation are preserved by virtue of the fine-grained sediment that surrounds and fills the fossils. Skeletal tissues were extensively preserved in only one specimen (PM TGU 2017-24/130, Fig. 5A, B), from which a ground section was prepared using an Isomet low speed saw. The surface of the section was prepared for imaging a number of times using a graded series of carborundum papers, then polished using 0.6  $\mu$ m diamond paste, and subsequently etched using 0.5% orthophosphoric acid for periods of 15 minutes to 1 hour. The prepared surface was then coated with gold and colloidal graphite before being imaged using a Hitachi S-3500N scanning electron microscope in secondary electron mode, with an acceleration voltage of 20 kV.

Despite repeated preparation, the dorsal dermoskeleton, which was exposed on a natural fracture in the rock, did not etch (Fig. 6A); it appears to have undergone diagenetic alteration. F6 Only the largest-scale histological structures are preserved, such as coarse vascular canals (Fig. 6), but it is nevertheless possible to discern that the dorsal dermoskeleton of *llemoraspis kirkinskayae* exhibits the classical three-layered organisation: a superficial layer of tubercles, underlain by a highly vascularised middle layer, and floored by a layer of more compact tissue. Nothing more can be determined because of the poor preservation of the histology.

However, in the sediment that fills the space beneath the dorsal dermoskeleton are series of non-articulated scales that are, nevertheless, organised in a broad row that extends across the width of the dorsal dermoskeletal headshield (Fig. 6). From their organisation and their arrangement, with superficial tubercles oriented in the opposite direction to those of the dorsal dermoskeleton (Fig. 6A), we interpret them as the ventral plates that floor the oralobranchial chamber of Ilemoraspis. The structure of these scales is not well preserved but, nevertheless, shows some fine-scale histological features such as mineralised (intrinsic) fibre bundles and the spaces left by cell processes (Fig. 6B-F). The component scales are small, though their size can only be judged from their exposed extent, the greatest of which is approximately 1.8 mm wide and 500 µm in thickness; most of the scales are smaller than this and, in particular, they are much thinner, composed of no more than a single row of tubercles and a uniting sheet of

FIGURE 5. *Ilemoraspis kirkinskayae.* **A**, **B**, mix of dorsal and ventral surface dermoskeletal tesserae in dorsal view, PM TGU 2017-24/130; **C**, **D** detail of ornament of dermoskeleton, PM TGU 1028-3-2/130. **Abbreviations: dgr**, dorsal groove; **dtes**, dorsal tesserae; **intar**, inter areal canals; **lc**, lateral sensory canal; **mfo**, median field ornamentation; **ors**, scales or tesserae covering the ventral floor of the oralobranchial chamber; **prdg**, fine parallel ridges; **vrim**, ventral rim of the cephalic shield. Scale bar equals 1 cm.



FIGURE 6. Etched ground sections through the cephalothoracic dermoskeleton of *llemoraspis kirkinskayae*, PM TGU 2017-24/130. **A**, overshot of dorsal dermoskeleton (no histological detail) and underlying partially articulated ventral dermoskeletal plates; **B**, **D**, moulds of cone-shaped tubercles comprising the ventral dermoskeletal plates showing natural endocasts of the pulp cavities and their associated vascular canals; note the thinness of uniting dermal plate; **C**, **E**, **F**, marginal ventral dermal plate inverted from A. **E**, higher magnification of the upper left in C, showing faint dentine tubules present in the tubercles which ramify from the pulp cavity (upper field), lamellar structure and extrinsic fibre matrix clear in the lower left of the growing margin of this plate; **F**, higher magnification of upper right in C, showing highly vascularised (subaponeurotic vascular plexus) bone (lower field) and overlying tubercles with faint traces of dentine tubercles. Relative scale bar equals: A, 850  $\mu$ m; B, 252  $\mu$ m; C, 745  $\mu$ m; D, 100  $\mu$ m; E, 200  $\mu$ m; F, 252  $\mu$ m.

bony tissue (Fig. 6B, D). The composition of the thinner scales is not well preserved, but heavily etched preparations revealed that each tubercle possessed a pulp cavity. The thickest of the scales show clear evidence that the tubercles are composed of dentine: long, thin spaces representing the sites of cell processes radiate from a central pulp cavity that shows evidence of centripetal lamellar growth. Branching of the cell processes cannot be discerned but, if it does occur, these ramifications were limited to the immediate subsurface of the tubercles. The matrix of the superficial layer, where present, is poorly preserved histologically, but in places, small, round spaces are observed that probably represent the sites of extrinsic fibre bundles (Fig. 6E). The base of the scales is characterised by a layer of lamellar tissue, showing evidence of marginal growth (Fig. 6E).

From what little can be discerned of its gross structure, the

dorsal dermoskeleton of *Ilemoraspis kirkinskayae* compares well with that of other osteostracans, except the tremataspidoids where the superficial layer of the dermoskeleton, though composed of dentine, is not composed of discrete tubercles (Denison, 1947; Donoghue and Sansom, 2002; Donoghue et al., 2006). There is also a well-developed vascular middle layer, which is otherwise much reduced in thyestiids more broadly. The only histological detail available is for the ventral scales of the headshield and thus there is little comparable information from other osteostracans. In fact, the available data are limited to the cursory description of gross histology of *Balticaspis* by Otto and Laurin (2001a) who, nevertheless, showed that the ventral tesserae were very thin and dominated by slender coniform tubercles as in *I. kirkinskayae* and, based on the description by Janvier and Arsenault (1996), the cornuae and body scales in *Escuminaspis laticeps*.

# LATERAL LINE SYSTEM

The trunk region of the Osteostraci was previously known in detail only from the faunas of the United Kingdom, Ringerike, Norway, as well as Miguasha and Mackenzie Mountains, Canada. The exceptionally preservation conditions in Khakassia have enabled the elucidation of the extensive lateral line system in not only the head of *Ilemoraspis kirkinskayae* (Fig. 7) but also in the body, thus having ramifications for the evolution of this character in the vertebrates. PM TGU 3002/130 (a middle body section preserved in lateral aspect) reveals a single lateral line extending along its length in the form of an open groove, reaching posteriorly at least the narrowest point of the caudal peduncle (Fig. 4C–F). The specimen is unfortunately incomplete and it is therefore not possible to establish either the anteriormost point of the lateral line or whether it is continuous with the lateral line system of the head.

Previous studies of the body and tail region of the Osteostraci (Stensiö, 1932; Heintz, 1939, 1967; Belles-Isles, 1986) have not observed a lateral line extending onto the body, but this is possibly "due to the imperfect state of preservation in which the squamation of the Cephalaspids is generally found" (Stensiö, 1932:71). A possible exception is *Tremataspis*, from the Silurian of Estonia. Whilst *Tremataspis* displays no trace of a lateral line on the scales of the trunk, it displays paired anteroposteriorly directed lateral lines on the ventral and dorsal surfaces of its extended abdominal division of the sheld (Robertson 1937; Janvier, 1974, 1985a; pers. obs.). Given the length of the abdominal division in *Tremataspis*, the dorsal and ventral lateral lines could

be considered as homologous with dorsal and ventral lateral lines of the trunk. In *I. kirkinskayae*, it is clear that the extended trunk lateral line is not the dorsal lateral line but it is not clear whether it is homologous to the main or ventral lateral line of jawed vertebrates. Whilst it is in a ventral position, it occurs dorsal to the ventrolateral ridge and as such could represent the main lateral line. The condition in *Tremataspis* (presence of a ventral line and absence of a main line) would indicate that *I. kirkinskayae* has an extended ventral lateral line.

Taking into account the condition in *Tremataspis*, linked with new information from *I. kirkinskayae* and the poor preservation of the trunk of other Osteostraci, we can reconstruct the common ancestor of Osteostraci as having possessed one, or more likely two, sensory canals extending caudally onto the trunk. This condition therefore differs from either of the living relatives of the Osteostraci; three trunk lateral lines are observed in crowngroup gnathostomes (dorsal, main, and ventral) and a single dorsal trunk lateral line is observed in lampreys (Northcutt, 1985, 1989). The osteostracan condition must be viewed in the light of the condition in related clades to understand the evolution of the trunk lateral line.

The sensory line system of thelodonts consists of either closed canals that communicate with the external surface via wellcharacterized pore scales or open grooves. Articulated specimens of *Phlebolepis* (Märss, 1979) demonstrate pore scales arranged in a regular row, forming a single extended dorsal line extending onto the trunk and tail. *Sphenonectris turnerae* (Wilson and Caldwell, 1998) possesses an open groove between scales, forming a single extended dorsal line extending onto the



FIGURE 7. Reconstruction of *llemoraspis kirkinskayae*. A, lateral aspect with total length as estimate only; **B**, cephalic shield in dorsal view; **C**. cephalic shield in ventral view.

trunk and tail which descended ventrally towards the caudal lobe. In Sacabambaspis (an arandaspid, Pteraspidomorphi), a single ventral lateral line is observed to extend onto the trunk (Gagnier, 1993) whilst in Anglaspis (a heterostracan, Pteraspidomorphi) a single lateral line is observed extending onto the caudal region (Blieck and Heintz, 1983), but it is not possible to determine whether it is a dorsal or main lateral line. The condition is unknown for galeaspids due to the paucity of articulated specimens. Within placoderms, dorsal and main lateral lines are observed to extend onto the trunk, whilst the condition of the ventral line is unknown (Northcutt, 1989). The ancestral condition for gnathostomes is considered as three trunk lateral lines due presence of all three lines (main, ventral and dorsal) in Osteichthyes and Chondrichthyes (Northcutt, 1989) and developed main and ventral lines in acanthodians (Watson, 1937). Combining the new data for the Osteostraci and existing data for other stem-gnathostome clades, it is possible to utilise parsimony to reconstruct scenarios of the evolution of trunk sensory lines

■ (Fig. 8). A single dorsal trunk line exists in the common ancestor of vertebrates. A second trunk lateral line (either main or ventral) appears in either the common ancestor of Osteostraci and jawed vertebrates, or the common ancestor of Galeaspida, Osteostraci and jawed vertebrates, depending upon the condition in galeaspids. A third trunk lateral line (either main or ventral, depending upon the homology of the osteostracan line), appears in the common ancestor of jawed vertebrates. The ventral condition in *Sacabambaspis* is resolved as homoplastic. This scenario of trunk lateral line evolution is consistent with the step-wise establishment of the gnathostome body plan before the origin of jaws, in the stem-gnathostomes (Forey, 1995; Donoghue and Purnell, 2005).

## PHYLOGENETIC AFFINITY

Ilemoraspis kirkinskayae has a unique mix of features and a number of apomorphies that make it difficult to place in any phylogenetic framework for the Osteostraci. It has previously been considered as incertae sedis or possibly allied with *Tannuaspis* (Afanassieva and Janvier, 1985; Janvier, 1985c). *Tannuaspis* and *Ilemoraspis* share widely spaced orbits, the lateral and median field shapes and orientations, round nasohypophysial openings, and absence of a pineal plate. This relationship is supported by



phylogenetic analyses of the Thyestiida (Fig. 9A, B; Mark-Kurik 🖪 and Janvier, 1997; Sansom, in press), but there are several characters contradicting it. *Tannuaspis* possesses a long cephalic abdominal division with continuous lateral cephalic endoskeletal extensions and lacks paired fins, whereas *I. kirkinskayae* clearly possesses freestanding cornua and paired fins. Ornamentation also differs between the two, with *Tannuaspis* exhibiting closely set, pointed and costulate tubercles whilst *I. kirkinskayae* has fine parallel sinuous ridges but this character state is highly homoplastic within the Osteostraci.



FIGURE 8. Lateral line evolution on the trunk. Phylogeny based on Donoghue and Smith (2001). Terminal nodes are *Sacabambaspis* (an arandaspid, left) and *Anglaspis* (a heterostracan, right) for the Pteraspidomorphi, *Tremataspis* (left) and *Ilemoraspis* (right) for the Osteostraci and finally, Placodermi and crown Gnathostomata for jawed vertebrates. Dashed represents uncertain condition. Note that the intermediate position of the bottom line in the common ancestor of the Osteostraci and jawed vertebrates (and in *Ilemoraspis*) reflects uncertainty with respect to the homology of this line, to the main or ventral lateral line.

FIGURE 9. Phylogenetic placement of *llemoraspis*. **A**, strict consensus of Mark-Kurik and Janvier (1997) resolving *llemoraspis* as sister to *Tannuaspis*, within the tremataspidoids; **B**, strict consensus of Sansom (in press) also resolving *llemoraspis* as sister to *Tannuaspis*, within the tremataspidoids; **C**, alternative placements of *llemoraspis* as either (A) sister to *Tannuaspis*, within tremataspidoids, or (B) sister to all other thyestiids.  $A_{1,2}$ ,  $B_{1,2}$  and C are characters supporting the respective placements and are discussed in text.

If we accept the sister-group relationships of *Tannuaspis* and *Ilemoraspis* (Tannuaspidinae), the logical phylogenetic placement is within the Tremataspidoidei. *Tannuaspis* has often been allied with or placed with the tremataspidoids, within the Thyestiida, by reason of its long abdominal division and lack of paired fins (Halstead Tarlo, 1967; Afanassieva and Janvier, 1985; Janvier, 1985a; Mark-Kurik and Janvier, 1997; Sansom, in press) yet *I. kirkinskayae* lacks these features. Whilst *I. kirkinskayae* lacks these thyestiid and tremataspidoid characters, it does possess a number of other thyestiid and tremataspidoid characters including short lateral fields, a medial course of the infraorbital lateral line, endolymphatic duct openings external to median field, and lack of a horizontal caudal lobe.

In addition to the Thyestiida, it would also be prudent to compare Ilemoraspis with the small number of other osteostracan taxa that survived into the Middle and Late Devonian. Afanassiaspis (known from isolated tesserae only) and Balticaspis from the Eifelian of Baltic Europe both share with I. kirkinskayae a reduced basal layer and loosely connected tesserae (Otto and Laurin, 1999, 2001a, b). Trewinia from the Eifelian of Scotland also has tuberculated, loosely connected tesserae (Janvier and Newman, 2005). Escuminaspis and Levesquaspis from the Frasnian of Quebec are the latest surviving osteostracans (Arsenault and Janvier, 1995; Janvier and Arsenault, 1996). Escuminaspis (Alaspis being a junior synonym [Janvier pers. comm. 2001]) possesses large mushroom-shaped tubercles and again, loosely connected tesserae. Levesquaspis possesses rounded tubercles, but unlike the other Middle or Late Devonian osteostracans, lacks tessellation. It is therefore evident that *I. kirkinskayae* shares with all Middle or Late Devonian Osteostraci a reduced basal layer and loosely connected tesserae (with the exception of Levesquaspis). It would be incorrect to consider these taxa as a distinct clade because of dermoskeletal similarities alone because many other anatomical differences exist among them. Escuminaspis, Levesquaspis, Trewinia, and Balticaspis (known from the posteroventral cephalic shield surface only) share a semicircular, broad cephalic shield bearing broad cornua with posterior cornual plates along with a potential absence of lateral fields. Conversely, the cephalic shield of I. kirkinskayae is not semicircular, being longer than broad, bears thin cornua, and has lateral fields. Thus dermoskeletal reduction has occurred independently in the more recent Osteostraci-once in I. kirkinskayae and at least once in the others.

A preliminary consideration of the two most plausible and parsimonious phylogenetic placements for Ilemoraspis is shown in Figure 9C upon the backbone of a recent parsimony analysis (Sansom, in press). For placement A, Ilemoraspis is placed as sister taxon to Tannuaspis within the tremataspidoids (Mark-Kurik and Janvier, 1997; Sansom, in press). This system is consistent with lateral field shape and abdominal scales (A1), interorbital distance, nasohypophysial shape, and pineal plate loss  $(A_2)$ . In light of the new information regarding *I. kirkinskayae* and the inconsistencies with Tannuaspis sister-group relationships, an alternative placement outside the Thyestiida, placement B, is considered. This system is consistent with dermoskeletal condition  $(B_1)$  as well as loss of paired fins, loss of cornua, and location of the endolymphatic ducts  $(B_2)$ . In both systems, placement of Ilemoraspis is consistent with its possession of thyestiid characters of a medial infraorbital line and horizontal caudal lobe absence (C). A more taxonomically comprehensive approach is required to firmly place Ilemoraspis phylogenetically, but in the absence of a rigid phylogenetic framework for the Osteostraci, this is not currently possible.

## THE PARADOX OF ILEMORASPIS

As stated, *Ilemoraspis kirkinskayae* is unusual within the Osteostraci, not only with regard to its anatomy and age, but also its

paleogeographic location on the West Sayan Terrane unit. Here, it would have been separate from all other Osteostraci, save *Tannuaspis* and *Tuvaspis* on the Tuva-Mongol Terrane. The Tuva-Mongol Terrane and the West Sayan Terrane unit collectively belong to the Altaids (Peri-Siberian Terranes). The new anatomical information brought to light by the Khakassia specimens in some respects contradicts our understanding of osteostracan evolution and paleobiogeography. This paradox is best demonstrated when considering the two possible placements of *Ilemoraspis* within osteostracan phylogeny as either sister to *Tannuaspis* within the tremataspidoids (Fig. 9; placement A) or within the cornuate Osteostraci as a basal thyestiid (Fig. 9; placement B).

Placement A (Tannuaspidinae) is highly consistent with paleobiogeographic data. Osteostracan diversity can be neatly divided into two faunal provinces as defined by Young (1981): (1) the cephalaspid province restricted to the Euramerican continent which yields the majority of osteostracan diversity; and (2) the tannuaspid province restricted to the Altaids, represented by endemic Tannuaspis, Tuvaspis, and Ilemoraspis. The osteostracan fauna from Severnaya Zemlya (Mark-Kurik and Janvier, 1995) is considered as part of the cephalaspid province because of the association between the Kara terrane and Euramerica (Cocks and Torsvik, 2005, 2007). These two Siluro-Devonian faunal provinces are separated by not only the Ural Ocean, but also by the continent of Siberia (Scotese and McKerrow, 1990; Cocks and Torsvik, 2007). The amphiaspid province of Siberia is dominated by amphiaspid heterostracans and has not yielded any osteostracans so far. With Tannuaspis, Tuvaspis, and Ilemoraspis occurring as a monophyletic clade, a minimum of only one intercontinental dispersal is required within the Osteostraci. The Tannuaspidinae hypothesis is thus paleogeographically parsimonious. It is also consistent with the anatomical features uniting Tannuaspis and Ilemoraspis (Fig. 9: A1, A2). Prior to the discovery of the new Khakassia specimens, the condition of the cornua and fins of Ilemoraspis was unknown and thus the Tannuaspidinae could therefore be considered as an Altaid clade, without paired fins and cornua (Blieck and Janvier, 1999), placed within the tremataspidoids (Fig. 9:placement A).

It is clearly demonstrated here, however, that Ilemoraspis kirkinskayae possessed not only long, divergent cornua, but also well-developed paired pectoral fins. Placement A, therefore, requires us to envisage either multiple losses of paired fins and cornuae or a reversal from a finless condition to a finned condition i.e., Ilemoraspis has a finless ancestor and regains paired fins. Considering the complexity of the paired fins and the rarity of regaining paired appendages from a limbless ancestor in the vertebrates (unknown with a possible exception occurring within snakes [Coates and Ruta, 2000; Apesteguía and Zaher, 2006]), it seems highly unlikely that such a reversal could have taken place. Furthermore, multiple losses of paired fins and cornuae (at least 4) would be far from parsimonious. The logical placement for Ilemoraspis is, therefore, amongst the non-tremataspidoid cornuate Osteostraci, most parsimoniously as a basal thyestiid (Fig. 9:placement B). This requires only one state change (the minimum) with regard to osteostracan paired pectoral fins: loss in the tremataspidoids (B<sub>2</sub>). This placement is, however, inconsistent with paleobiogeography. This second scheme requires two separate intercontinental dispersals from the cephalaspid province to the tannuaspid province, one each for Ilemoraspis and Tannuaspis. The geographic separation in itself implies that multiple dispersals are improbable, but considering the restrictive nature of osteostracan ecology (shallow freshwater, estuarine or lagoonal environments), in combination with the high degree of endemism exhibited by the group generally (Young, 1981; Janvier, 1985b; Dineley, 1988; Young, 1990), two such intercontinental dispersals are highly improbable.

An alternative to the two proposed scenarios would be to

retain monophyly of Tannuaspidinae (*Tannuaspis* + *Ilemoraspis*) but for Tannuaspidinae to be sister to all other thyestiids. This scenario is consistent with paleobiogeography (monophyly of all Altaid forms) but is still inconsistent with paired fins, this time requiring two losses of paired fins within the Osteostraci. Furthermore, it is inconsistent with the many tremataspidoid characters of *Tannuaspis* such as long abdominal division, position and shape of lateral fields, 'sel' canal reduction. This last scheme is therefore rejected.

*Ilemoraspis* therefore represents a paradox. The conflict between anatomy and paleobiogeography makes it necessary to envisage either two separate intercontinental dispersal events occurring in a restricted, endemic group (placement B) or an unprecedented reversal to a paired appendage condition from a finless ancestor (placement A).

Furthermore, Ilemoraspis kirkinskayae is exceptional amongst the Osteostraci with regard to its stratigraphic range. The osteostracan genera currently known to have the longest stratigraphical ranges are Diademaspis and Benneviaspis. Species from each genus are known from middle Lochkovian to early Emsian deposits (Janvier, 1985c; Blieck and Cloutier, 2000; Uchman et al., 2004). There is a certain level of ambiguity about the stratigraphic ranges of I. kirkinskayae, for both the holotype and the new specimens described here. The former is known from the late Givetian and the latter known from the late Pragian to middle Emsian. The ghost range between the two (late Emsian, Eifelian and early Givetian) is not surprising given that the Emsian beds in the area are unconformably overlain by the Givetian and furthermore, that the area is poorly characterised generally. What is dubious is such a long range for one species, by far the longest for any osteostracan species or genus. The principal differences between the holotype and the new specimens relate to the extreme distortion of the former. Despite what the stratigraphic range suggests, there is no anatomical basis to believe that they are two different species, much less that they are different genera. A thorough review of the stratigraphy of the region, especially the type locality, is necessary to establish whether this surprising range is real or an artefact.

Both of the problems of ghost ranges and conflict between anatomical homology and biogeography are due to non-random sampling. Better sampling of Asiatic Russia will hopefully yield more osteostracan localities and more osteostracan taxa and as such expand the biogeographic range of the group.

## CONCLUSIONS

It is now possible to reconstruct in much more detail the anatomy of the unique and previously poorly characterized species Ilemoraspis kirkinskayae. A lateral line is observed extending far back onto the trunk-a novel observation for the Osteostraci. This enables the proposal of a scenario of stepwise evolution of trunk lateral lines. Like the majority of Osteostraci and contrary to some interpretations, I. kirkinskayae possessed well-developed paired pectoral fins and long, divergent cornua. It shares with its geographic neighbour Tannuaspis small lateral fields, widely spaced orbits, and, uniquely within the Osteostraci, a round nasohypophysial opening. As such, Ilemoraspis represents a paradox for osteostracan evolution, requiring us to envisage either two separate intercontinental geographic dispersal events in a group displaying endemism and restrictive ecology or, conversely, an unprecedented reversal from a finless condition to a finned one. The paradox is a likely consequence of an incomplete fossil record of Asiatic Osteostraci.

## ACKNOWLEDGEMENTS

Thanks go to Philippe Janvier (Paris) both for initially bringing together S. Rodygin and R. Sansom and for helpful discussion over interpretation of certain specimens. Thanks also go to Simon Powell for the photographs in Fig. 4A. This research has been made possible by NERC PhD studentship funding (NER/ S/A/2004/12682) as well as funding from the Royal Society (international incoming short visit grant) and the Palaeontological Association (travel award), both of which have enabled exchange visits between Tomsk and Bristol.

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Submitted July 31, 2007; accepted January 28, 2008.



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