A NEW BUCHANOSTEID ARTHRODIRE (PLACODERM FISH) FROM THE EARLY DEVONIAN OF THE URAL MOUNTAINS

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ABSTRACT—A new primitive brachythoracid arthrodire, *Uralosteus bashkiricus* gen. et sp. nov., is described from two Emsian (late Early Devonian) localities in the Ural Mountains of the Autonomous Republic of Bashkortostan, Russia. The holotype includes bones of the skull and trunk armor associated with numerous scales from one individual, which facilitates the study of isolated microremains. The dermal ornament of distinctive tuberculate ridges suggests a relationship to *Errolosteus* Young, 1981 from the Emsian of southeastern Australia, but neither form is well enough known for this to be strongly supported in a character analysis. Some isolated placoderm bones with ridged ornament from southeastern Australia are figured, and interpreted to belong to a new form of williamsaspid rather than to *Errolosteus*. The new genus *Uralosteus* is referred to the family Buchanosteidae, defined by a unique overlap arrangement of the posterior lateral onto the anterior dorsolateral plate of the trunk armor. Buchanosteids, as a basal brachythoracid group, are a key to understanding the phylogeny of that clade. The type genus *Buchanosteus* comes from southeastern Australia, but it is now evident that the family was widely distributed in shallow marine environments during the Emsian.

INTRODUCTION

The arthrodire genus *Buchanosteus* was erected by Stensiö (1945) for a specimen from the Emsian limestones around Buchan, in Victoria, Australia, that had previously been illustrated and interpreted by Hills (1936) as '*Coccosteus osseus*'. Other remains of this form were described from limestones of similar age in the Burrinjuck Dam area near Canberra by White (1952, 1978), White and Toombs (1972), and Young (1979). Long (1984a, 1991) illustrated further buchanosteid material from the type locality in Victoria. Other placoderm groups from both areas include petalichthyids and acanthothoracids (Young, 1978, 1980, 1985; Long, 1984b; Long and Young, 1988; Findlay, 1996). There are several osteichthyans in the fauna (actinopterygians: Schultze, 1968; Basden et al., 2000a; dipnoans: e.g., Thomson and Campbell, 1971; Campbell and Barwick, 2000), and acanthodians, chondrichthyans, onychodontids, and thelodonts are also known from vertebrate microremains (Ørvig, 1969a; Giffin, 1980; Basden, 1999; Basden et al., 2000b; Lindley, 2000).

White (1952) erected a family, Buchanosteidae, for the genus *Buchanosteus*, and since that time various other primitive brachythoracid arthrodires have been provisionally assigned to this family or have been considered to be closely related, including new taxa from the Burrinjuck Dam fauna erected by White (1978) and Young (1981). Amongst these is the monotypic genus *Errolosteus* Young 1981, which is characterised by distinctive ridged ornament. Phylogenetic analyses by Lelièvre (1988, 1995) suggested a close relationship between *Errolosteus* and *Buchanosteus*, but the type material of *Errolosteus* comprised only an incomplete skull and a few disarticulated trunk armor bones, so many morphological aspects have been poorly known.

A limestone sample from the Devonian of the Ural Mountains given long ago by the late Professor D. V. Obruchev (Moscow) to E. M. K. was considered to contain small fragments of the well-known arthrodire *Holonema*, which is also characterised by ridged ornament. Details provided with this specimen record that it was collected in 1934 by geologist E. I. Falkova from the Vyazovaya Formation in the Belaya River region of Bashkortostan (Bashkiria) in the southern Urals (Fig. 1). After a long period of preparation using mechanical and then chemical (acetic acid) methods, the bones extracted from the limestone revealed ornament closely similar to *Errolosteus* described by Young (1981) from Australia. In 1986 another specimen of probably the same form was collected from Emsian strata on the Inzer River (Takata Formation), about 150 km to the north (Fig. 1), by A. G. Ivanushkin (Chelyabinsk), who sent it to Tallinn for study. This specimen is a detailed impression preserved in a coarse silicified gritstone. Both Russian specimens were brought to Australia in 1995, when the current descriptions were prepared based on comparisons with the type material of *Errolosteus*.

The Lower Devonian Takata and Vyazovaya formations extend along the western slope of the Ural Mountains and the eastern border of the Russian (East European) platform. Miospore assemblages have been assigned to the late Emsian *Retusostrilites clandestinus* (RC) Zone and those from the lower Takata Formation to the *Apiculiretusispora divulgata* var. *plicata* (DP) Subzone (Avkhimovitch et al., 1993). The Takata and coeval Irgisly regional stages (formations) and the Vyazovaya Regional Stage (Formation) have been correlated with the interval from the *gronbergi* to the early *serotinus* conodont zones by Sapel'nikov et al. (2000). The Takata Formation in the northern Urals has also yielded a trematapsid osteostracan (Mark-Kurik and Janvier, 1997). The Taemas Limestone of southeastern Australia spans the *dehiscens* to *serotinus* conodont zones of the Emsian (Basden et al., 2000b).

Institutional Abbreviations—Specimens described or cited in the text are housed in the Institute of Geology at Tallinn Technical University (prefix Pi), the Geology Department, Australian National University, Canberra (prefix CPC or ANU), and the Museum of Victoria, Melbourne (prefix NMV).

Anatomical Abbreviations—ADL, anterior dorsolateral plate; **AL**, anterior lateral plate; **AMV**, anterior median ventral plate; **C**, central plate; **c**, corner marking external contact of PL and AL plates; **cd**, glenoid condyle of dermal neck joint; **cfADL**, area overlapping ADL plate; **cfPDL**, area overlapping PDL plate; **cfSP**, area overlapping SP plate; **csc**, central sensory canal; **d.end**, external opening of endolymphatic duct; **gr.pbl**,

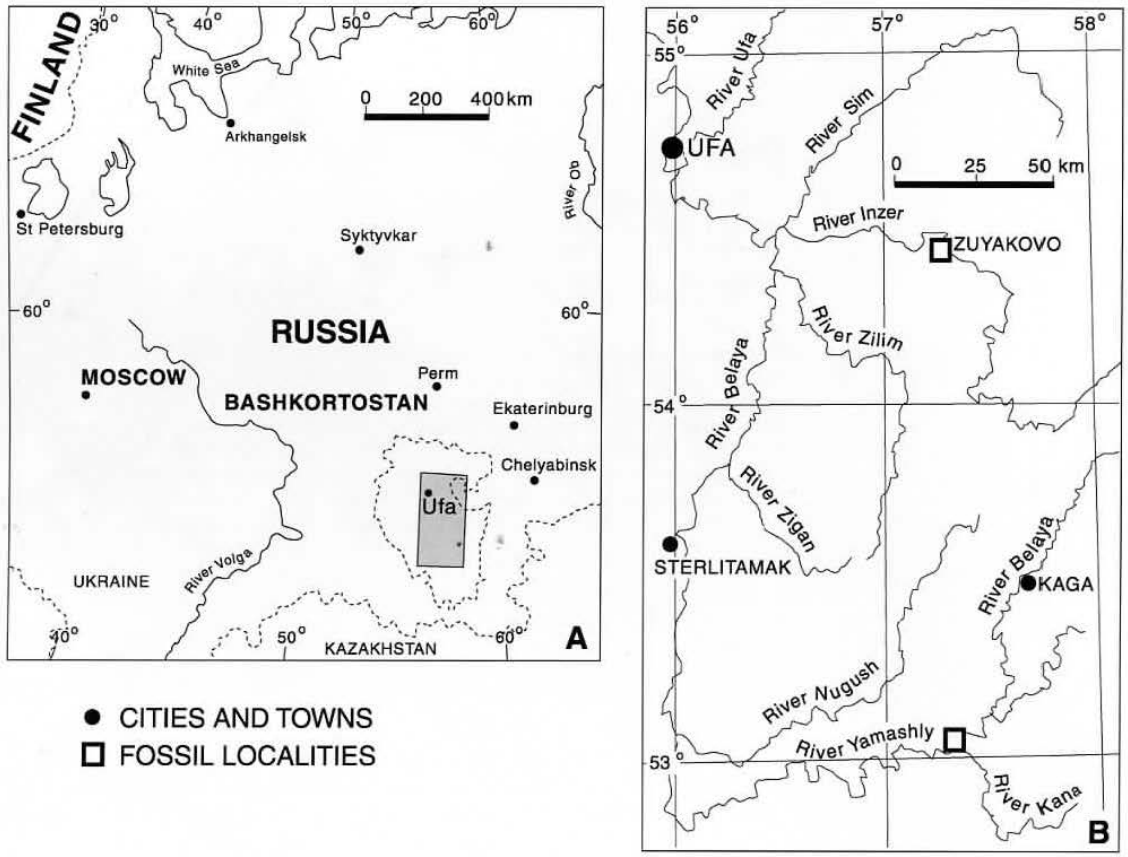

FIGURE 1. **A**, location of Bashkortostan (Bashkiria) in the European part of Russia, and adjacent countries. **B**, locality map for the River Belaya basin, central Bashkortostan, where the two specimens were collected.

groove for postbranchial ridge of AL plate; **if.r**, infranuchal ridge; **if.pt**, infranuchal pit; **IL**, interolateral plate; **laf**, articular fossa for dermal neck joint; **k**, keel on MD plate; **lc**, main lateral line sensory canal; **ld**, dorsal branch of sensory groove on ADL plate; **M**, marginal plate; **MD**, median dorsal plate; **m.dep**, median depression; **mp**, middle pitline; **Nu**, nuchal plate; **no**, notch; **n.th**, nuchal thickening; **oaAL**, area overlapped by AL plate; **oaC**, area overlapped by C plate; **oaIL**, area overlapped by IL plate; **oaMD**, area overlapped by MD plate; **oaNu**, area overlapped by Nu plate; **oaPL**, area overlapped by PL plate; **oaPNu**, area overlapping or overlapped by PNu plate; **oaPVL**, area overlapping or overlapped by PVL plate; **occ**, occipital cross-commissure; **pap**, para-articular process; **pect**, embayment for pectoral fin; **PM**, postmarginal plate; **pmc**, postmarginal sensory groove; **PNu**, paranuchal plate; **pp**, posterior pitline; **pro**, obstantic process of AL; **PtO**, postorbital plate; **soa**, subobstantic area; **SP**, spinal plate; **vpr**, median ventral (carinal) process on MD plate.

SYSTEMATIC PALEONTOLOGY

Class PLACODERMI
Order ARTHRODIRA
Family BUCHANOSTEIDAE White, 1952

Diagnosis—Primitive brachythoracids with anterior dorsolateral plate overlapped by posterior lateral as well as anterior lateral and median dorsal plates.

Remarks—The above character was number 17 in the list presented by White and Toombs (1972:404–406) to enlarge on their diagnosis of a new order 'Migmatocephala' containing a single family Buchanosteidae. This higher taxon was defined as 'euarthrodires shewing both well developed dolichothoracid and brachythoracid characters', with the 'anterior part of skull-roof with separate rostro–pineal bone and broad, short preorbital plates with complete mesial contact.' They also stated: 'pattern of remainder of plates of skull-roof, of the sensory system and of the known body-plates typically brachythoracid' (White and Toombs, 1972:381). They considered the endocranium to be the 'generalized form for both groups' of arthrodires (dolichothoracids and brachythoracids), and thus omitted endocranial characters from their diagnosis, although White (1952) had originally defined the family Buchanosteidae on such features.

The definition adopted here follows Mark-Kurik's (1991) usage to refer isolated ADL plates from Severnaya Zemlya to the family Buchanosteidae. This seems to be the only character which stands out as a synapomorphy by outgroup comparison to phlyctaeniid and actinolepid arthrodires, and is proposed as a provisional defining feature of the group. The interrelationships of 'buchanosteids' are considered further below in discussion.

URALOSTEUS BASHKIRICUS, gen. et sp. nov.
(Figs. 2–9)

1998, 'new buchanosteid from the Urals,' Burrow and Turner, pp. 677, 687

1999, 'new buchanosteid with close affinity to *Errolosteus*,' Burrow and Turner, p. 214

Material—1. Holotype. Associated bones, all more or less

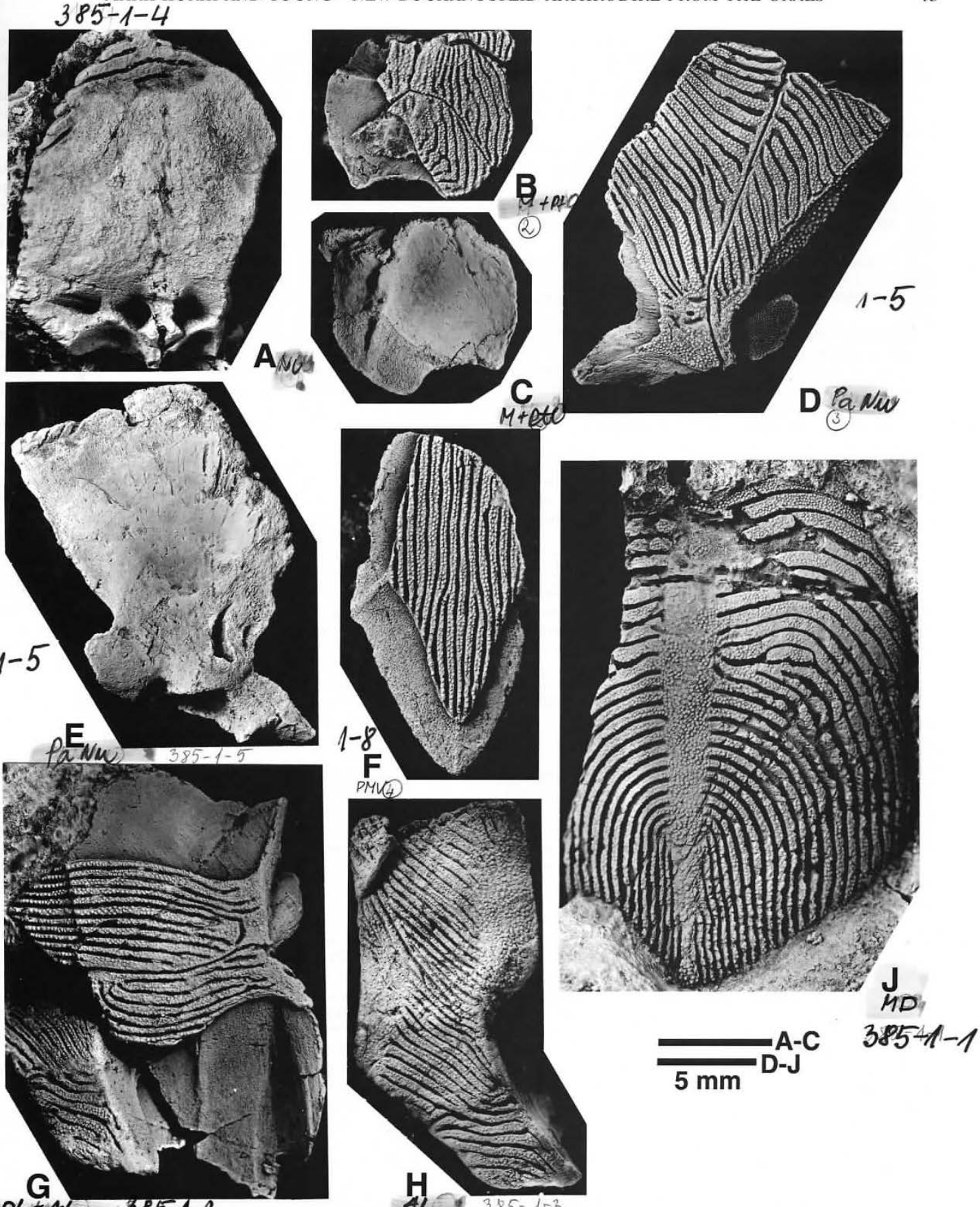

FIGURE 2. *Uralosteus bashkiricus* gen. et sp. nov. Holotype (Pi 1291). **A**, Nu plate in internal view with impression of ornament partly seen. **B**, **C**, right M plate with portion of the PtO in external and internal views. **D**, **E**, right PNu plate in external and internal views. **F**, incomplete PMV plate, external view. **G**, incomplete right ADL and AL plates, external view (partly prepared). **H**, incomplete right AL plate, external view. **J**, incomplete MD plate, external view.

incomplete, assumed to come from one individual: Pi 1291a (median dorsal plate), 1291b (right anterior dorsolateral), 1291c (right anterior lateral), 1291d (nuchal), 1291e (right paranuchal), 1291f (fragment of left paranuchal), 1291g (right marginal with small attached part of right postorbital), 1291h (posterior median ventral), 1291i–s (scales).

2. Pi 1292, impression of a left anterior lateral plate.

Locality and Horizon—1. Single limestone sample collected as a loose block in the bed of the Yamashly River upstream from the village of Akbulatova, Belaya River Basin, Southern Ural Mountains, Vyazovaya Formation (Early Devonian, Emsian).

2. Coarse gritstone sample from the right bank of the Inzer River, 0.5 km downstream from the village of Zuyakovo, Southern Ural Mountains, Takata Formation (Early Devonian, Emsian).

Diagnosis—Brachythoracid arthrodire characterised by dermal ornament of flat ridges carrying up to 3–4 rows of tubercles separated by deep grooves, with ridges generally at least twice as wide as grooves; ornament tending to concentric on dorsal surface (nuchal and median dorsal plates), with more longitudinal ridges laterally, and ventrally in midline; regions of fine crowded tubercles over ossification centers, extended as median zone broadening towards anterior margin of median dorsal plate; nuchal plate with convex posterior margin; paranuchal with prominent para-articular process, oval-shaped articular fossa, and subobstantic area covered with fine tubercles; postorbital plate of skull relatively large; sensory groove crossing anterior and posterior dorsolateral plates roughly parallel to lateral margin of median dorsal plate, without posteroventral sensory groove to posterior lateral plate; anterior lateral plate high and narrow with vertical pectoral margin, indicating pectoral embayment rather than fenestra; postbranchial lamina with four denticulate ridges curving ventromesially from postbranchial notch.

Remarks—Differences in morphology described below seem sufficient to separate this new form at the generic level, but the similar strongly ridged ornament suggests a relationship to *Errolosteus goodradigbeensis* Young, 1981, previously placed within the Buchanosteidae (see Comparisons). Some differences in ornament pattern between these two taxa may be either generic or specific differences, for example, the radiating ridges at the anterior margin of the nuchal and paranuchal plates in *Errolosteus goodradigbeensis* (concentric in *Uralosteus bashkiricus*), and the generally narrower ridges, about twice the width of intervening grooves, in *Errolosteus*. In addition, the AL of *Errolosteus* is lower and broader, with a more horizontally oriented pectoral margin. The holonematids also have ridged ornament, but the ridges vary much more in width, the grooves of the ornament are more shallow, and there are numerous differences in bone shape (e.g., Miles, 1971; Nessov and Mark-Kurik, 1999). Some Eifelian *Holonema* species completely lack ridges (Otto, 1998). *Uralosteus bashkiricus* evidently had a relatively large postorbital plate and probably a short marginal plate. In contrast, in several other primitive brachythoracids (e.g., *Buchanosteus*, *Antineosteus*, *Taemasosteus*) a small postorbital was combined with an elongate marginal plate. The absence of a posteroventral sensory groove branch on the trunk armor is a point of difference to both *Coccosteus* and *Buchanosteus*.

Description

The holotype of *Uralosteus bashkiricus* comprises associated but disarticulated bones of the skull and trunk-armor listed above, all more or less incomplete, together with a number of scales. All are assumed to come from one fish. They were extracted from a single limestone sample found in the bed of the river, with several fragments exposed and therefore abraded or water-worn. Some bones are badly fractured, and could not be completely removed from the matrix using acetic acid without risk of disintegration. However the paranuchal (**PNu**), marginal (**M**), anterior dorsolateral (**ADL**), anterior lateral (**AL**) and posterior median ventral (**PMV**) plates have been extracted using this technique.

The second specimen of the AL plate is preserved as an impression showing the same distinctive ornament, and in shape and proportions corresponds closely to the preserved portion of the anterior lateral (AL) plate in the holotype, with only minor differences. Based on present knowledge, it is assumed also to belong to *Uralosteus bashkiricus*.

Skull—The nuchal (Nu) plate is still in the rock, with mainly the inner surface exposed. Anteriorly it is weathered through to expose the base of the ornamental ridges (Fig. 2A). Posteriorly it shows paired infranuchal pits separated by a median ridge and process (**if.pt**, **if.r**, Fig. 3A), in an arrangment rather similar to that figured for *Taemasosteus* by White (1978:fig. 78), except that the posterior margin is more convex. *Buchanosteus* is differently developed here (Young, 1979:fig. 2), and this region is not known for *Errolosteus goodradigbeensis*. In front of the pits the bone is thick and flat, but the inner surface is waterworn and contact faces for the PNu plates are not clear. Only the posterior margin of the Nu is complete.

The right paranuchal (**PNu**; Fig. 2D, E) shows the external overlap for the Nu, and the internal contact face for the marginal (M) is clearly seen inside its lateral corner. The inner surface is weathered and the mesial edge which underlapped the Nu is missing, but the depression for the supravagal process is visible, and the prominent para–articular process is well preserved (**pap**; Fig. 3D). The articular fossa for the dermal neck joint (laf) is incomplete mesially, but the lateral portion shows it had a deep oval shape similar to that figured for *Taemasosteus* by White (1978:fig. 78). This structure in *Buchanosteus* is more elongate (Young, 1979:pl. 1C), at least in small specimens. The anteromesial corner of the PNu is incomplete, and the visceral surface shows no sign of the contact face for the central (C) plate. In Figure 7 this region has been restored on the assumption that the PNu had similar length to the Nu, with some conformity in the ornament. Externally the PNu shows the normal brachythoracid arrangement of sensory grooves (lc, pp, occ; Fig. 3B), around the external opening for the endolymphatic duct (d.end). Anteriorly the ridges of ornament run from the margin of the subobstantic area (soa) across the sensory groove. This is different to the radiating arrangement on an isolated PNu which Findlay (1996:fig. 5) compared to *Errolosteus goodradigbeensis* because of its similar ornament. However, the anterolateral corner is the only part of the PNu preserved in the holotype of *E. goodradigbeensis*. The subobstantic area (soa), which fitted under the obstantic process of the AL plate when the head was depressed, is covered with fine tubercles.

The right marginal (M) plate (Fig. 2B, C) has a complete posterior margin showing the overlap for the PNu and C plates (oaPNu, oaC; Fig. 3C). There is also a small portion of the postorbital (PtO) plate attached on the broken anterior margin, with a very clear but slightly displaced suture. The mesial end of the suture seems to turn forward, suggesting an anterior process of the M overlapping the PtO along the sensory groove, as occurs in *Coccosteus cuspidatus* (e.g., Miles and Westoll, 1968:fig. 9a) and many other brachythoracids. The inner surface of the M shows a very clear contact face for the postmarginal (PM) plate (Fig. 2C), with the inframarginal crista in the normal position, running just beneath the postmarginal canal (pmc; Fig. 3C). The lateral margin of the M plate is not quite complete, but there was evidently a notch at the M/PtO suture as in many other placoderms.

The preservation of the PtO/M suture shows that the M plate

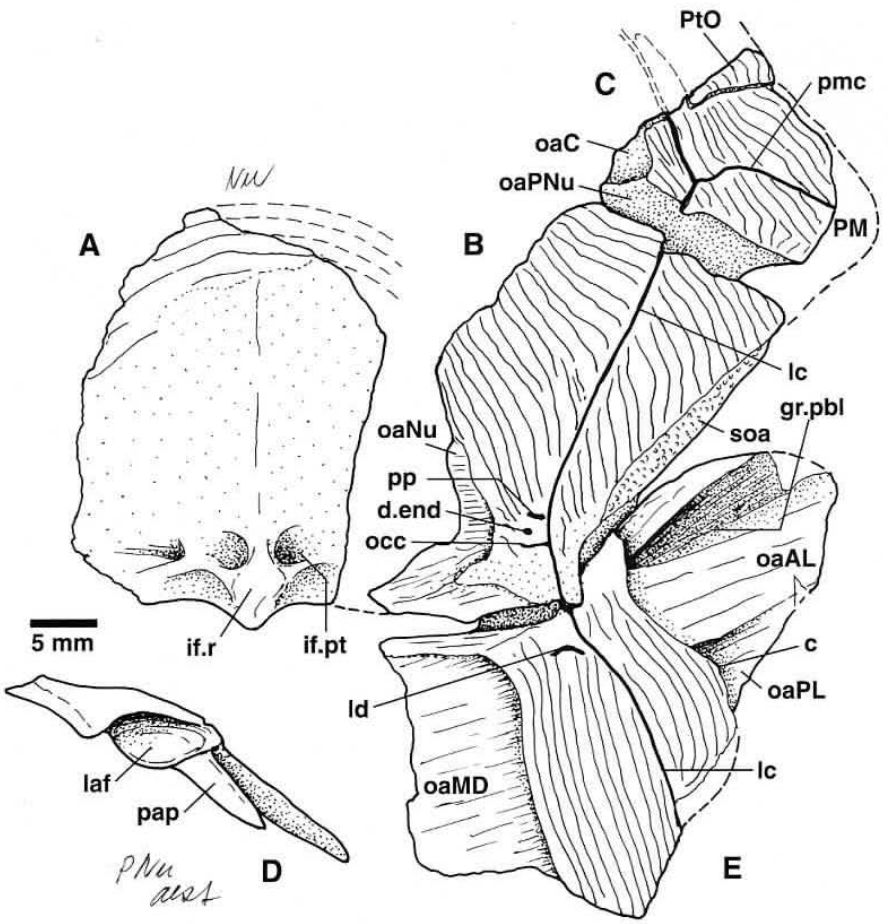

FIGURE 3. *Uralosteus bashkiricus* gen. et sp. nov. Holotype (Pi 1291). **A–C**, preserved skull bones in approximate relative positions against the ADL (**E**). Based on camera lucida drawings (flattened) of PNu articulated against ADL, and overlap relations with Nu and M/PtO. **D**, right PNu in posterior view.

was unusually short, and much shorter than in any of the arthrodires known from the Taemas-Buchan fauna. This part of the skull is not known in *Errolosteus goodradigbeensis*, but even forms with very short, broad skulls such as *Burrinjucosteus* as restored by White (1978:fig. 70) had much longer marginals than did *Uralosteus*. To give its skull outline reasonable proportions, a relatively large PtO must be restored, as seen in eubrachythoracids such as *Coccosteus* (Miles and Westoll, 1968). This might be a more advanced feature compared to other Emsian arthrodires (e.g., *Buchanosteus*, *Antineosteus*, *Taemasosteus*), all of which combined a very long M with a short PtO plate.

Trunk Armor—The acid-prepared external surface of the median dorsal (MD) plate displays the striking ornament pattern characteristic of this new genus, with tuberculate ridges concentrically arranged around the posteriorly placed ossification center, from which a median zone of dense tubercles runs forward to the anterior margin (Fig. 2J). The left side of the MD is broken off, and the visceral surface of the right side was partly exposed before collection, so is water worn and abraded (Fig. 5A). However, it shows the extent of the contact faces for the anterior and posterior dorsolateral plates, with the latter slightly more extensive than the former (cfADL, cfPDL; Fig. 6B). The left and right laminae of the MD plate meet at a low angle, with no suggestion of a median dorsal elevation (Fig. 6A). The median ventral keel is partly preserved (k; Fig. 6A), but posteriorly is incomplete, although a median ventral process can be assumed (vpr; Fig. 6B). The slightly abraded posterior margin has been restored on the assumption that not much is missing, and the shape of the anterolateral corner (Fig. 6B) is based on the corresponding overlap area on the ADL.

The right ADL was closely associated with the anterior lateral (AL) plate (Fig. 2G) before extraction from the matrix to reveal its inner surface (Fig. 7C). The dorsal margin of the bone is broken, but its shape is indicated by the contact face on the MD (Fig. 6B). The ventral and posterior margins are almost complete, with the posterior margin assumed to have been slightly convex beneath the lateral line groove, as indicated by the adjacent ridged ornament (Fig. 3E). The dermal neck joint is normally developed, with the articular condyle having a similar shape to the fossa on the PNu (cd; Fig. 6A). The lateral line groove (lc; Fig. 3E) runs back from the neck joint roughly parallel to the edge of the overlap area for the MD, with a short dorsal branch which turns posteriorly (ld) and is then lost in the grooves of the ornament. The dorsal branch presumably continued as a superficial pitline towards the ossification center of the MD while the main canal passed posteriorly onto the PDL. In contrast to *Coccosteus* (Miles and Westoll, 1968:fig. 43) or *Buchanosteus* (White and Toombs, 1972:fig. 24), there is no strong groove passing posteroventrally to the posterior lateral (PL) plate. The ventral overlap area for the AL shows normal development for a brachythoracid, with a strong groove to receive the postbranchial ridge of the AL plate (gr.pbl; Fig. 3E), but *Uralosteus* is unusual in having a distinctive posterior overlap area for the PL plate (oaPL). This feature was illustrated by White and Toombs (1972:pl. 7), who considered it to

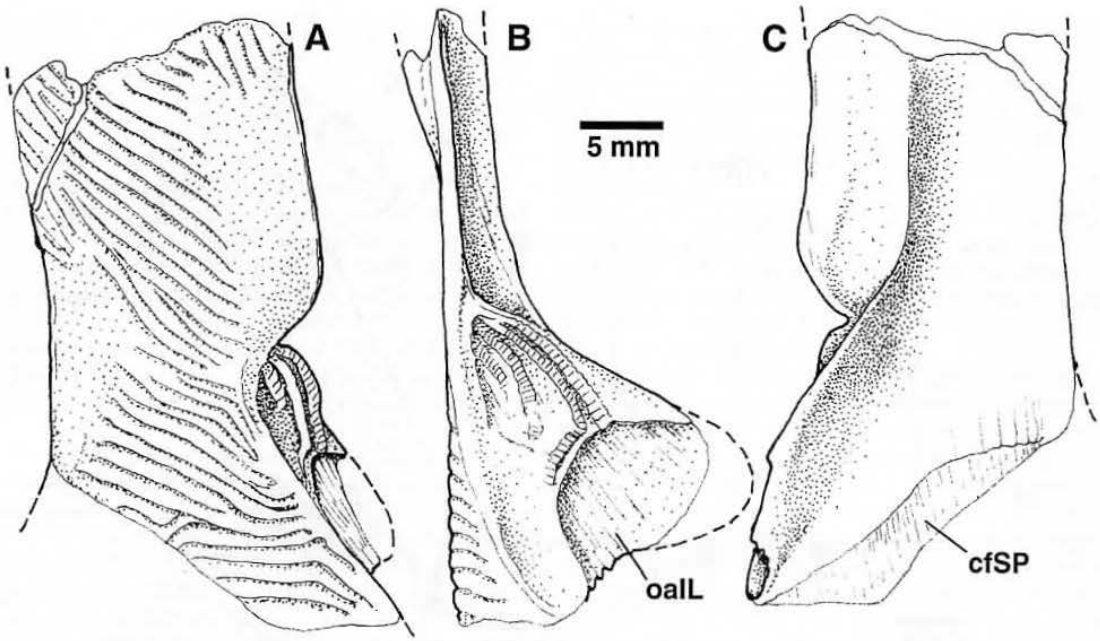

FIGURE 4. *Uralosteus bashkiricus* gen. et sp. nov. Holotype (Pi 1291). Incomplete right AL plate in external (**A**), anterior (**B**), and internal (**C**) views.

be characteristic of the taxon '*Parabuchanosteus murrumbidgeensis*' and of the family Buchanosteidae (see below). A small corner on the ventral border of the ornamented area (c; Fig. 3E) may mark the point where the external surfaces of the AL and PL met, or the overlapped lamina of the PL may have been entirely enclosed between the AL externally and the ADL internally (Fig. 7B). The present material does not permit a decision on this point.

The inner surface of the ADL is normally developed. There is a gently concave central surface behind the ridge running to the ventral corner as a thickening beneath the groove on the external surface for the post-branchial thickening of the overlapping AL plate. Posteriorly the contact face which overlapped the PDL plate (unknown) extends slightly above and below the ornamented posterior projection of the bone (cfPDL; Fig. 7C). Its ventral extent is marked by a slight notch, below which the posterior edge of the ADL is deeply depressed for the overlap of the PL plate.

The ADL was not described for *Errolosteus goodradigbeensis* by Young (1981), but an example from the Emsian limestones at Buchan, Victoria, was referred to *Errolosteus* cf. *E. goodradigbeensis* by Long (1984b) on the basis of similar ornament. This specimen differs in many respects from the ADL of *Uralosteus bashkiricus*, and we suggest below that it may not belong to a brachythoracid.

The anterior lateral (AL) plate of *Uralosteus bashkiricus* is represented by two specimens. The holotype yielded an incomplete right AL, now completely removed from the matrix (Fig. 4). Before preparation the dorsal portion of this bone was broken off at the level of the edge of the ADL (Fig. 2G), so much of the dorsal lamina is missing. It is also incomplete ventrally, but enough of the anterior and posterior margins is preserved to indicate its high and narrow shape. The postbranchial lamina is inflected inwards at almost a right angle to the external surface, and apparently only a small part of its mesial margin is missing (Fig. 4B). It lacks ornament except for four denticulate ridges, which curve ventromesially from the postbranchial notch and carry a special ornament of narrow, transverse elevations pointing ventrolaterally. Such ornament is seen on the postbranchial lamina of many placoderms, and may have served to restrict entry of parasites or floating debris through the opercular opening (Janvier, 1996). The second ridge turns to run around the edge of the overlap area for the IL (oaIL), which has a similar extent to this region in *Buchanosteus* (White and Toombs, 1972:pl. 8, fig. 4; pl. 9, fig. 2). Although the ventral edge of the AL is incomplete, it shows a clearly impressed contact face for the spinal (SP) plate that appears to have been rather extensive (cfSP; Fig. 4C). The posterior border of the bone is assumed to be complete and, as observed around the pectoral fenestra of other forms (e.g., *Buchanosteus*), carries a narrow groove along its edge. The orientation of the AL in the armor is uncertain, but direct comparison with the articulated trunk armor of '*Buchanosteus*' illustrated by Long (1984a) suggests that *Uralosteus* possessed a pectoral embayment rather than a fenestra. The AL and ADL can be placed together, but thickness of the dorsal preserved end of the postbranchial ridge on the AL indicates that there was little overlap of the preserved portion onto the ADL. This relative position of the two bones, as shown in Figure 7B, C, brings their complete anterior edges into alignment, and is assumed to approximate the correct arrangement. Thus there was probably a rather high and short lateral wall to the trunk armor somewhat as suggested for *Taemasosteus* by White (1978:fig. 111), which also evidently had a pectoral embayment. Whether this might be considered primitive or derived is discussed below.

The second example of the AL plate (Pi 1292; Fig. 5B) is an external impression from the left side that is fairly complete dorsally although it is possible that the posterodorsal corner was slightly broader than preserved. The ventral margin and almost all of the postbranchial lamina are missing, but most of the margin of the pectoral fenestra seems complete (pect; Fig. 6C). Just inside the postbranchial notch, the impression of the corner of the postbranchial lamina is preserved, showing two ridges directed inwards and downwards from the notch, essentially as in the holotype. The breadth across the bone to the postbranchial notch is also similar to that on the holotype, and the ornament is generally comparable, with zones of tuberculation replacing the ridges on the obstantic process and adjacent to

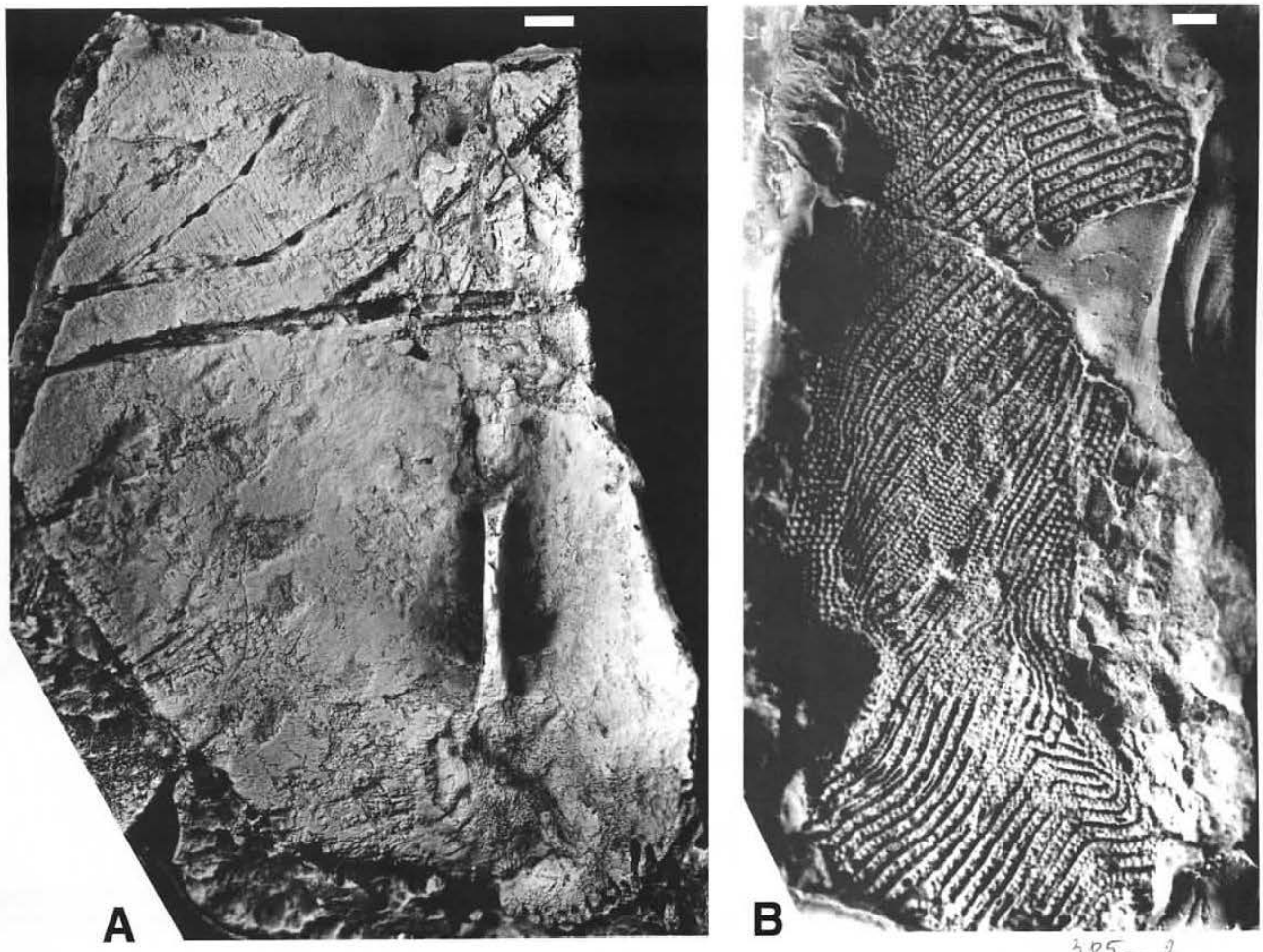

FIGURE 5. *Uralosteus bashkiricus* gen. et sp. nov. **A**, Holotype MD plate (Pi 1291), internal view. **B**, left AL plate (Pi 1292) in external view (latex cast). Scale bar equals 3 mm.

the presumed pectoral fenestra. However, these zones are more evident on the holotype (Fig. 2H) than on Pi 1292, which also has more steeply inclined ornamental ridges posteroventral to the postbranchial notch (Fig. 5B). Nevertheless, the similar high narrow form indicates that the second AL is correctly referred to *Uralosteus bashkiricus*. Quite different proportions for the AL were restored by Young (1981:fig. 13B) in *Errolosteus goodradigbeensis*, but a re-examination of that AL plate suggests that this may not be accurate. The dorsal margin of this specimen (CPC 16970) is incomplete, and by comparison with *Uralosteus* it seems that its dorsal lamina could have had higher and more narrow proportions, as for example in *Burrinjucosteus* from Taemas, which, if correctly assigned by White (1978:fig. 70), had a high, narrow AL combined with a broad skull roof. What is clear is that CPC 16970 differs from the two AL plates of *Uralosteus* in its sharply deflected supraspinal lamina (see Young, 1981:fig. 12B), giving the pectoral margin on the bone a more horizontal orientation than in Pi 1292. This character was included by Young (1981) in the diagnosis of the genus *Errolosteus goodradigbeensis* and remains a valid character for separating the two genera. An overlap area for the spinal plate along the ventral margin of the AL plate in *Errolosteus* was identified by Young (1981:fig. 17) as a possible synapomorphy with *Burrinjucosteus* and *Toombsosteus*, but neither specimen of *Uralosteus bashkiricus* has this region preserved.

The last bone known from the trunk armor of the holotype of *Uralosteus bashkiricus* is the posterior median ventral plate (Fig. 2F). This is incomplete anteriorly, but was apparently an elongate bone.

Attempted reconstructions of the preserved dermal armor of *Uralosteus bashkiricus* are given in Figure 7. The dorsal reconstruction of the skull roof and dorsal bones of the trunk armor (Fig. 7A) is based on camera lucida drawings of the PNu in position against the M plate, the ADL in position against the MD plate, and the right PNu and ADL articulated together across the dermal neck joint. The outline of the Nu was completed using its overlap area on the PNu, with the orientation of the partly exposed ornamental ridges giving some approximate idea of the plate margins. Overall width of the skull was constrained by the position of the dermal neck joint on each side. This was determined from the trunk-armor by graphically restoring the ADL with its condyle in horizontal orientation against the preserved portion of the MD. This portion includes the midline and permits a reconstruction of both dermal articulations (Fig. 6A). The trunk armor is shown slightly flattened, to display the shape of bones, and in life the ADL and AL would have closely followed the subobstantic margin of the PNu plate. The lateral and inner views of the known lateral plates of the trunk armor (Fig. 7B, C) are based on camera lucida drawings of the preserved parts of the right ADL and AL in position against each other.

Ornament—The known dermal bones of *Uralosteus bashkiricus* have a very distinctive ornament, comprising flat ridges carrying up to three or sometimes four rows of tubercles sep-

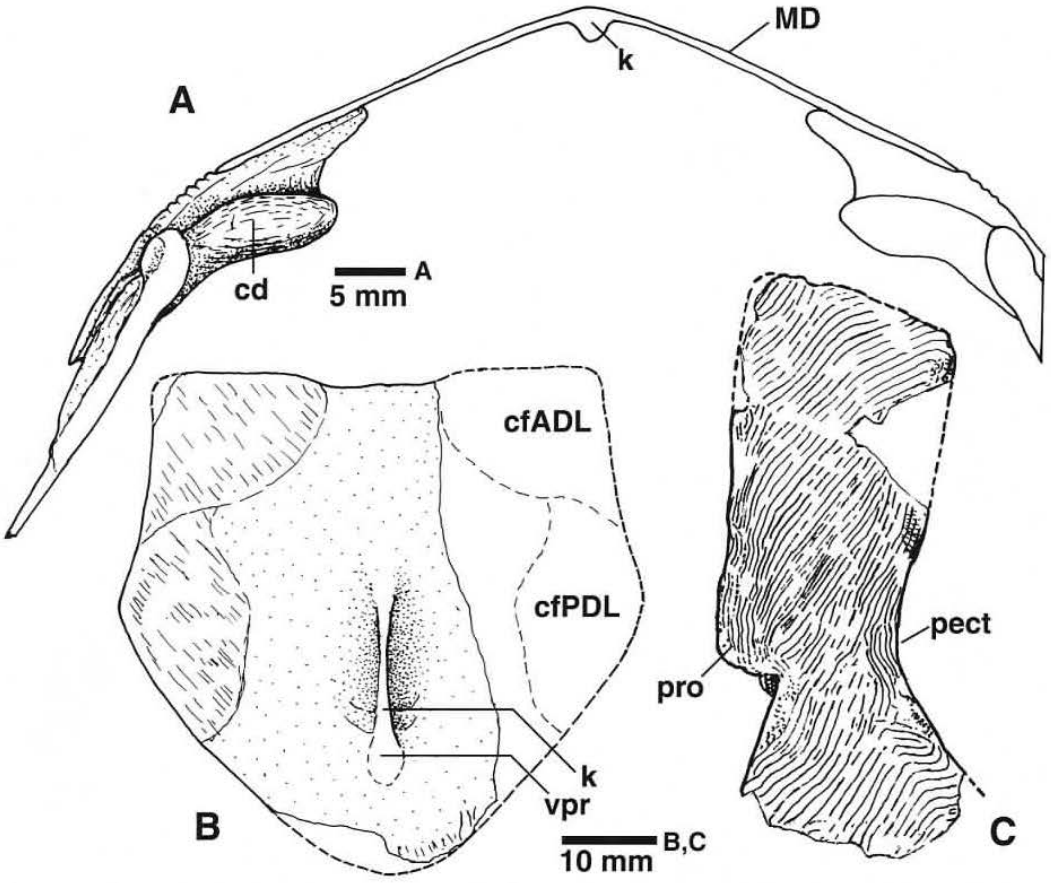

FIGURE 6. *Uralosteus bashkiricus* gen. et sp. nov. **A**, right ADL in anterior view, with MD and left ADL graphically restored using the horizontal orientation of the articular condyle (after the holotype, Pi 1291). **B**, MD plate (Pi 1291), internal view. **C**, left AL plate (Pi 1292) partly restored in external view.

arated by deep grooves. The ridges are generally at least twice as wide as the grooves (Fig. 10D). Along the broken anterior edge of the PMV the grooves are seen to be more narrow at the top and rounded ventrally to form an open tube which was slightly deeper than wide. The available specimens suggest a concentric arrangement of ornament on the dorsal surface, with more longitudinal ridges laterally and ventrally in the midline (PMV plate). The PNu, MD, and ADL also show regions of fine crowded tubercles over the ossification centers, with a strong median zone of tubercles on the MD broadening towards the anterior margin (Fig. 2J). Possibly this zone extended onto the skull, but this region of the Nu plate is not exposed.

Squamation—The matrix of the holotype included some 58 scales and scale fragments of consistent morphology that are assumed to come from this individual (Figs. 8, 9). Large and small scales (length 0.8–3.2 mm) differ somewhat in morphology. They typically show a high, narrow, tuberculate, external surface forming a longitudinal ridge, which in large scales is over twice as long as broad. The surface of the longitudinal ridge may be flat (Figs. 8E, 9F) or slope to the posterior (Fig. 9C), and in some is transversely arched with a single tubercle row forming a slight crest (Fig. 8C). The crowded tubercles are small and stellate with 6–8 radiating ridges, and tend to be slightly pointed towards the posterior. The radiating ridges on the tubercles are very clear on some scales (e.g., Fig. 8G), but generally are not sufficiently preserved to show details of the micro-ornament. The ventral scale surface consistently shows a concave base that forms a longitudinal groove, often wider anteriorly and narrow and deeper posteriorly (Fig. 8J). The groove may extend up the posterior margin and in some larger scales may notch the anterior margin (Fig. 8A–C). The larger scales tend to have the base expanded anteriorly to form an unornamented flange around the tuberculate ridge. The flange is concave dorsally with upwardly flared borders. Figure 8A shows a scale with a high central ridge, broken posteriorly and set on its flange-like base, which is much broader than the ornamented ridge. Tubercles are poorly preserved (perhaps worn), with about three across the top of the ridge. The best preserved and largest of this scale type (Fig. 8C) has five tubercles across the front, reducing to three rows posteriorly. The anterior tubercles are more elongate and posteriorly directed. The ornament extends down both sides of the ridge, and overall there are about 67 tubercles on this scale, a much higher number than on any of the various 'buchanosteid' scale types recently described by Burrow and Turner (1998). The base is broadest anteriorly, forming an unornamented rim which flares upwards on both sides, and is arched anteriorly over the antero-posterior groove on the ventral surface. Similar smaller scales shown in dorsal and right lateral views (Fig. 8B, E) both have a notched anterior margin. A smaller scale (1.7 mm long) illustrated in dorsal, ventral, and lateral views (Fig. 9A–C) has a somewhat wider and higher anterior portion and a narrower posterior portion that slopes down. The visceral side shows a posterior groove but anteriorly the surface is only slightly concave. The ornamented outer surface is much elevated in comparison with the thin unornamented scale margin, and the tubercles are worn. A larger example (Fig. 9D, E) shows a central foramen on the inner surface positioned towards the posterior, also seen in other

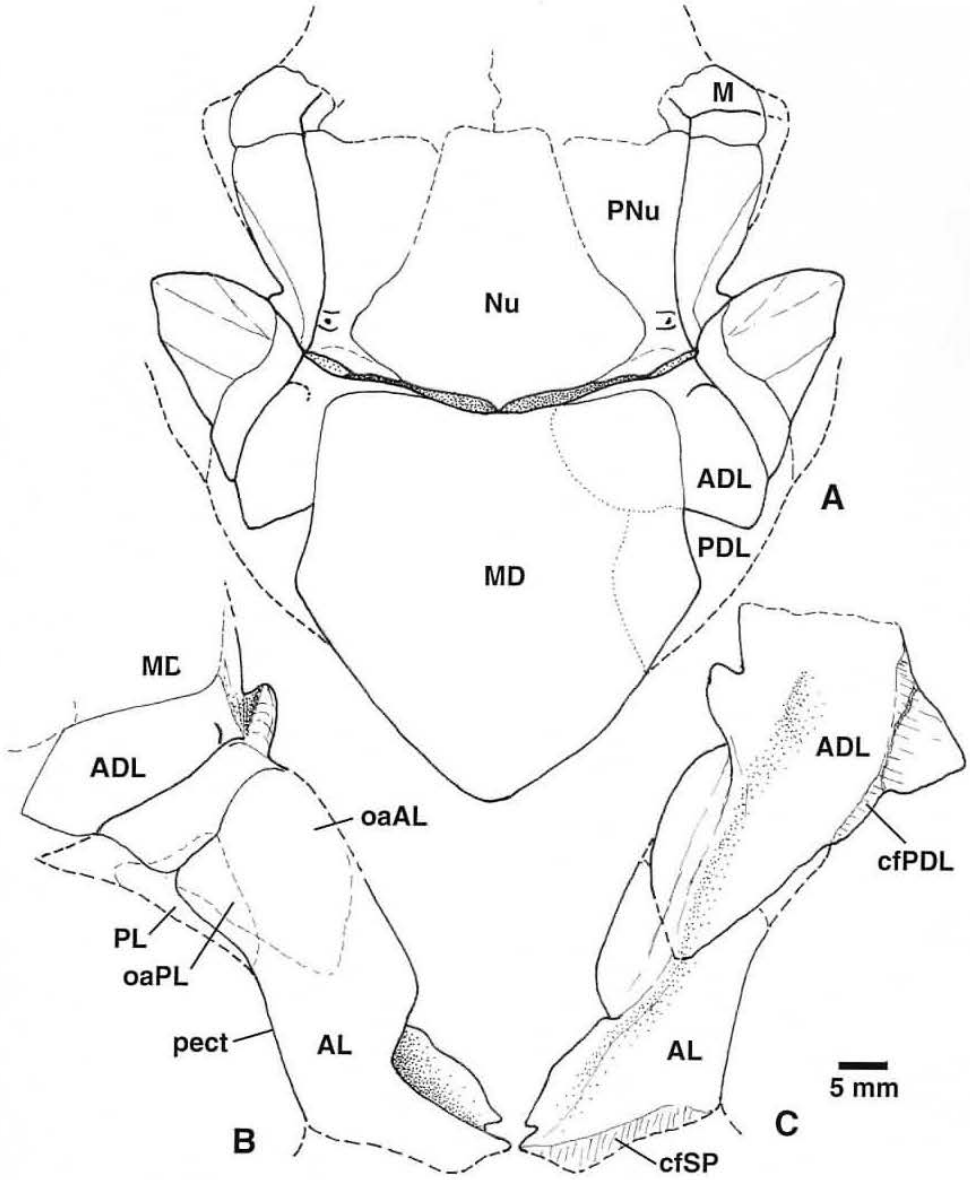

FIGURE 7. *Uralosteus bashkiricus* gen. et sp. nov. **A**, partial reconstruction of skull and dorsal trunk armor bones, dorsal view (after the holotype). **B**, partial reconstruction of the trunk armor in lateral view. **C**, right ADL and AL plates in approximate life position, internal view (after the holotype, Pi 1291).

scales where it may be double (Fig. 8J). Similar foramina are recorded in *Holonema* (e.g., the scale taxon *Artenolepis*; Lelièvre et al., 1983:pl. 2, fig. 1c; Trinajstic, 1999:fig. 6E).

A less common second scale type tends to be much smaller (Figs. 8D, 9G). This small scale lacks a flared base, and almost all of the lateral surface is ornamented with crowded small tubercles. Its ventral surface has a longitudinal groove, which is partly separated from a groove extending up the posterior margin, presumably indicating abutment against the scale behind.

A range of tuberculated scale types have been described from Devonian strata and assigned to various placoderm groups, but criteria for distinguishing major groups using information only from scales remain uncertain. This new specimen is one of the few known examples where scales are associated with large dermal bones that permit the owner to be definitely assigned to one of the major placoderm subgroups. It is important, therefore, to take account of the range of scale morphologies which can be expressed in material from one individual fish.

Because the dermal bones of *Uralosteus bashkiricus* have such a distinctive ridged ornament, one of the first questions is whether isolated scales also manifest this ridged condition. This seems to be the case in *Uralosteus*, but it is evidently not a general rule for other forms that have ridged ornament. In our small scale sample all scales have an antero-posterior groove on the inner surface, presumably formed on ridges in the dermis. For another arthrodire with ridged ornament, *Holonema*, this also seems to be the case with the '*Artenolepis*' scales described by Lelièvre et al. (1983), but not so in *H. westolli* according to the descriptions of Trinajstic (1999). In our sample most of the scales are larger, with an elongate tuberculate ridge and expanded flange-like base. We suggest that the ridge and base may have formed a ridge-and-groove pattern somewhat as in Figure 9H. This restoration shows the grooves between scales to be sinuous and of variable width, but this is also the case with the grooves on the dermal bones (Fig. 2). The smaller scales in our sample also have a ventral ridge, but no flange.

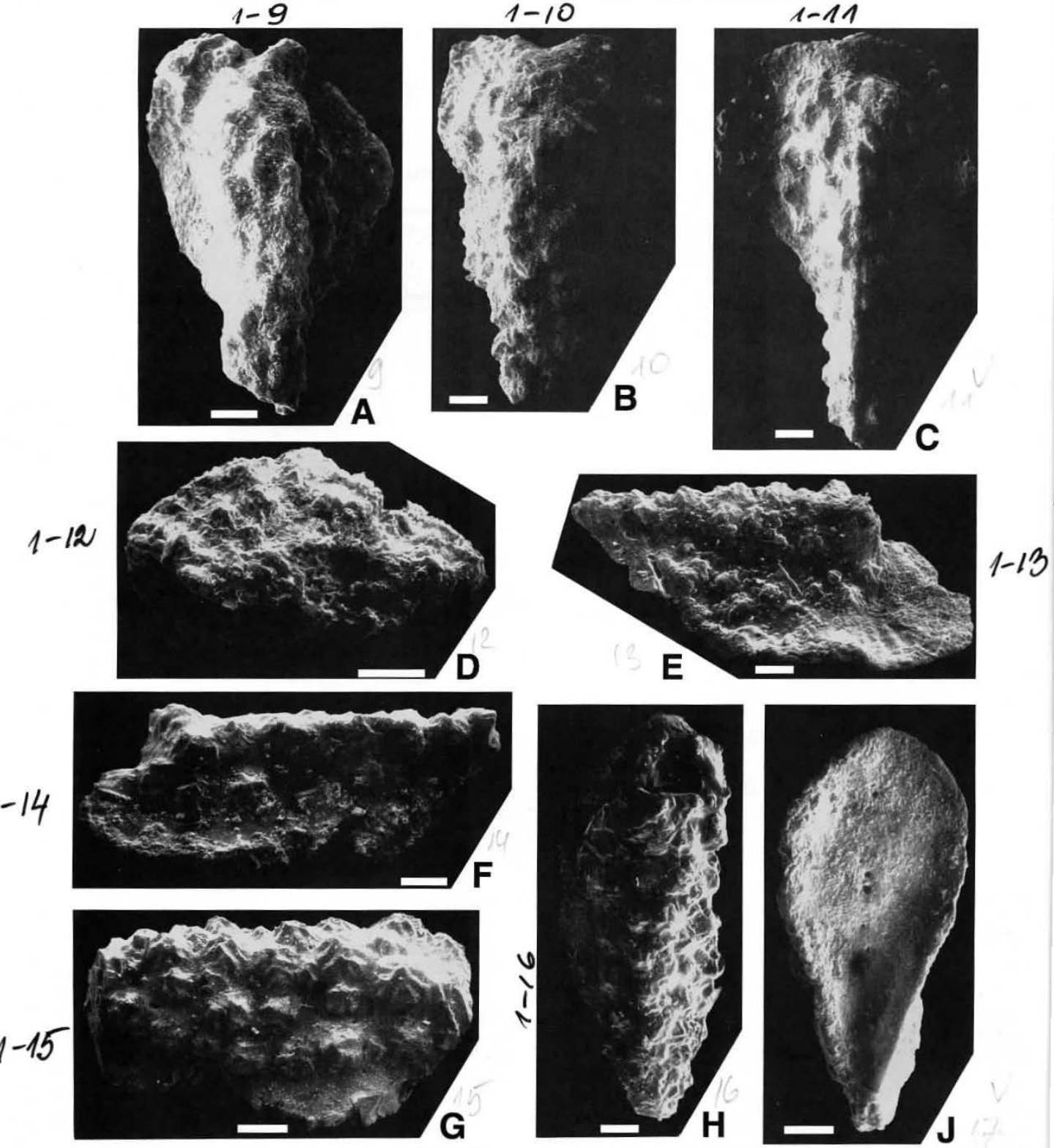

FIGURE 8. *Uralosteus bashkiricus* gen. et sp. nov. Body scales from the holotype (Pi 1291). **A–C**, **H**, external view. **D–G**, lateral view. **J**, internal view. Scale bar equals 0.25 mm.

They can be assumed to come from extremities where the ridges were smaller and more closely spaced. The intervening grooves would have contained soft tissue, but the lateral surfaces are ornamented, so they could not have been in contact. The *Artenolepis* scales assigned to *Holonema* cf. *radiatum* by Lelièvre et al. (1983) are sometimes fused to form elongate rectangular scales (see also Lelièvre et al., 1990:pl. 4F), presumably corresponding to the ridges on the dermal bones, but the shape of scales suggests that adjacent scales were in contact along their lateral margins, with the intervening grooves form-

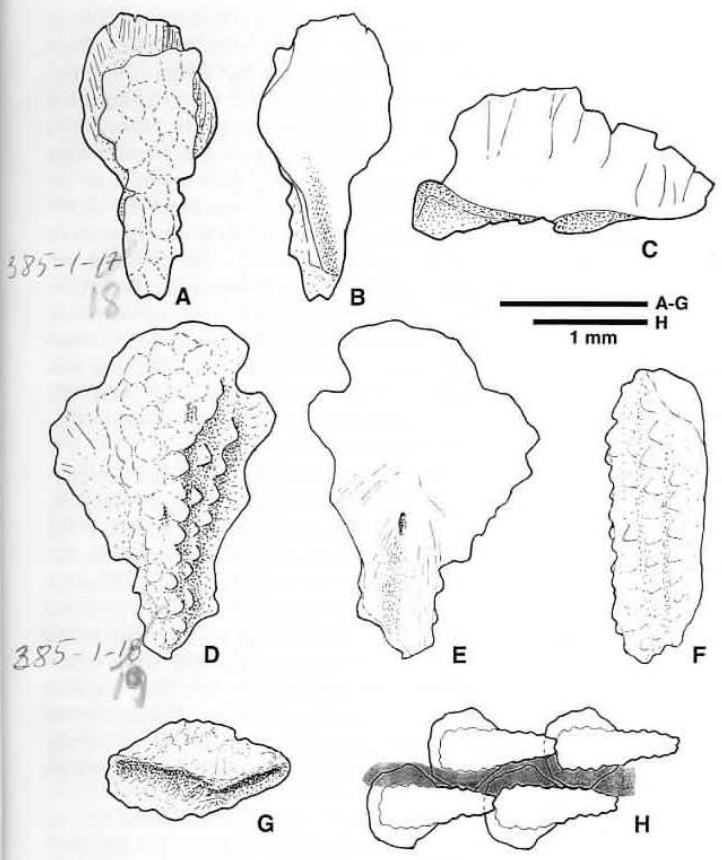

FIGURE 9. *Uralosteus bashkiricus* gen. et sp. nov. Body scales. **A–C**, Pi 1291r in dorsal, ventral and left lateral views. **D–F**, Pi 1291s in dorsal, ventral and left lateral views. **G**, Pi 1291, left ventrolateral view, showing ventral and posterior grooves (cf. Fig. 8D). **H**, attempted restoration of squamation, showing ridges, and intervening grooves (shaded).

ing enclosed tubes. In contrast, the scales of *H. westolli* are apparently rather differently developed. Two scale types were recorded by Trinajstic (1999), the more common being small rhombic scales, over 1 mm across, which covered the body surface in a 'pavement pattern', with polygonal scales near the fin bases, and only a few examples showing a distinct neck with a wider base than ornamented surface. The much larger second scale type (not figured) apparently resembles the fused triple scale illustrated by Lelièvre et al. (1983), but they are restricted to the region of the vertebral column and are interpreted as median dorsal ridge scales (Trinajstic, 1999:78). Trinajstic (1999) distinguished *Holonema* scales from those of *Coccosteus* and *Selenosteus* because they formed a 'definite . . . regular . . . pattern on the skin'. Characteristic features of *Holonema* scales seem to be their rectangular or rhomboid shape, as also illustrated by Lelièvre et al. (1983), and perhaps the rather flat ornamented surface. In contrast, the scales of *Uralosteus* apparently achieved a ridged pattern in the squamation in quite a different way, the only resemblance to *Holonema* scales being the consistent longitudinal groove on the visceral surface. Amongst the various 'buchanosteid' scales described by Burrow and Turner (1998), those illustrated as 'buchanosteid indet. gen. et sp. 2', with a flat to deeply concave base, may belong to a form with ridged ornament such as *Errolosteus*. We note, however, that the articulated trunk armor from Victoria attributed to *Buchanosteus* by Long (1984a:fig. 16F, H, I; 1991, pl. 2B) cannot be a buchanosteid as defined above and previously (White and Toombs, 1972; Young, 1979). The ADL in this specimen is not overlapped by the PL, and its more extensive ornamented part and sensory canal pattern are suggestive of *Coccosteus* and related forms (e.g., Miles and Westoll, 1968: fig. 30; Orvig, 1969b:fig. 2). Thus the 'buchanosteid' scales of Burrow and Turner (1998) derived from the Victorian specimen would seem to be misnamed (see also Burrow and Turner, 1999: 215). This shows that the evidence of associated dermal bones should be taken into account when assessing vertebrate microremains (note also that the Victorian specimen, NMV P159896, does not include any head plates, as erroneously stated by Burrow and Turner, 1998, erratum).

COMPARISONS

In *Uralosteus* all bones with the ornament preserved show a consistent type, with flat ridges ornamented with up to three rows of tubercles separated by deep grooves generally less than half the width of the ridges. The similar ornament in *Errolosteus goodradigbeensis* was described as 'closely spaced subparallel ridges carrying crowded tubercles in one, two or three longitudinal rows' (Young, 1981:257), with dense ornament of crowded tubercles, sometimes forming short anastomosing ridges over the ossification centers of bones (Young, 1981:fig. 9). A similar feature was described above for *Uralosteus*.

Nevertheless, there are obvious differences in ornament pattern where corresponding regions of the two taxa can be compared. For example the Nu plate on the skull has ridges radiating from the posterior ossification center to the anterior margin in *Errolosteus goodradigbeensis*, but in *Uralosteus* there is a strong concentric pattern, which is also evident on some other bones (e.g., the MD; Fig. 2J). It is noteworthy that the ornament ridges in *Uralosteus* are consistently at least twice as wide as the intervening grooves and may be up to four times as wide. In *Errolosteus goodradigbeensis* the ridges are narrower except in the referred PVL plate where a closely similar pattern to *Uralosteus* is seen (Fig. 10E). Reassessing the originally described specimens of *Errolosteus goodradigbeensis* in the light of the new material, we consider that the AL plate (CPC 16970) was correctly referred to the taxon because of close similarity in ornament to that on the holotype (ANU 21806). However, it now seems that the PVL (CPC 16971) could be referred to *Uralosteus bashkiricus* because it shows clear differences in ornament to the holotype and AL of *E. goodradigbeensis*.

An ADL from the Emsian limestones at Buchan in Victoria, with apparently similar ornament to *Errolosteus goodradigbeensis*, was illustrated by Long (1984b:fig. 4A), who referred it to the genus as '*Errolosteus* cf. *E. goodradigbeensis*'. The ornament, comprising ridges two or three stellate tubercles across (Fig. 10C), is very similar to that of another ADL from Burrinjuck (Fig. 10B). The Burrinjuck ADL resembles the Buchan specimen in its rounded posterior margin, posteroventral orientation of the lateral line groove, dorsal extension of the ornamented area in front of the overlap for the MD, and slight raised keel crossing the bone from the edge of the articular condyle to an angle on the posterior margin just above the notch for the sensory groove. The overlaps for the MD and AL are much less extensive than described above for *Uralosteus bashkiricus*, and the ornament has a concentric arrangement following the posterior margin, whereas in *Uralosteus bashkiricus* it is antero-posteriorly directed and runs off the posterior margin.

Both of these ADLs differ in many respects from the ADL of *Uralosteus bashkiricus*, and it is unclear whether they can reasonably be referred to *Errolosteus*. The presence of an articular condyle for the dermal neck joint indicates that they belong to a phlyctaenioid arthrodire rather than a petalichthyid (these also commonly display concentric ridged ornament; e.g., Young, 1978, 1985). Of other arthrodires in the Burrinjuck fauna with ridged ornament, *Williamsaspis bedfordi*, originally de-

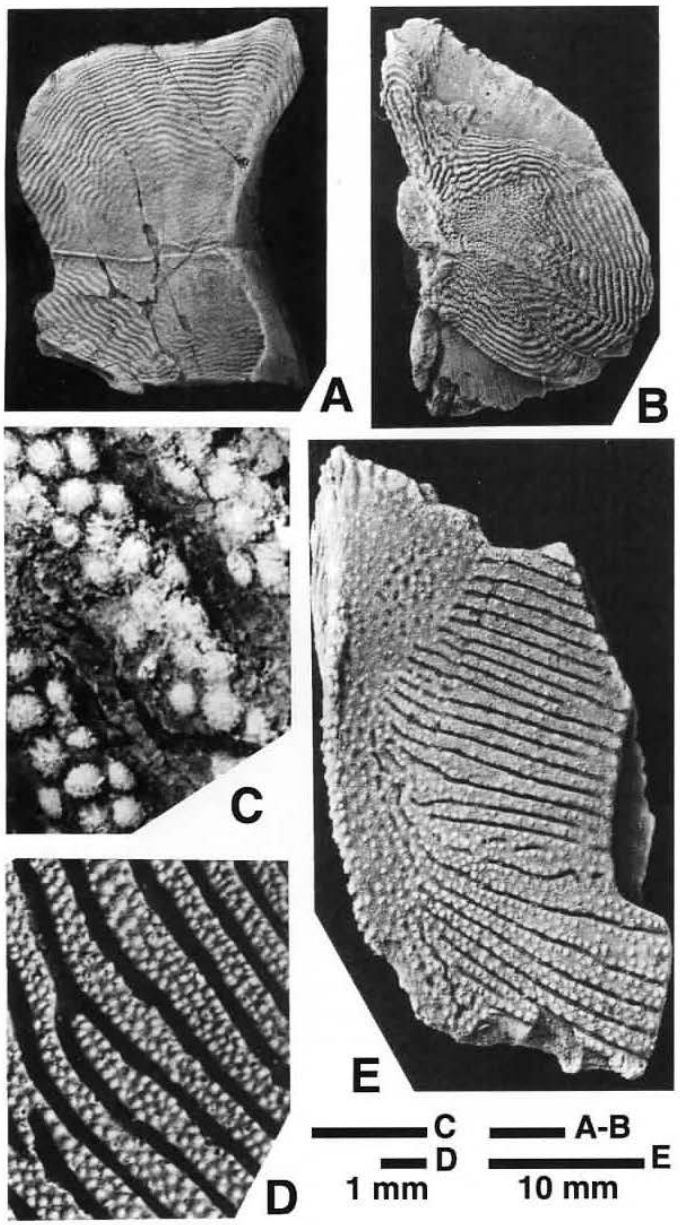

FIGURE 10. **A–C**, williamsaspid arthrodire, Early Devonian, southeastern Australia. **A**, right AL (ANU V1025), external view. **B**, left ADL (ANU V1865), external view. **C**, ornament detail on NMV 159894 (specimen illustrated by Long, 1984b:fig. 4A); **D**, *Uralosteus bashkiricus* gen. et sp. nov. Detail of ornament on right PNu plate (Pi 1294). **E**, *Uralosteus* sp. indet. right PVL plate (CPC 16971) previously referred by Young (1981) to *Errolosteus*.

scribed by White (1952), is a form known only by a single specimen, an incomplete but articulated trunk-armor. Although the holotype lacks ADL plates, *Williamsaspis* has been considered most likely to be some form of phlyctaenioid (e.g., Denison, 1978:65). The ornament of *Williamsaspis* was described as ridges apparently formed from a single row of stellate tubercles (White, 1952:pls. 26–29). However, an isolated AL plate (ANU V1025) of another presumably related form has an ornament of continuous ridges with no sign of discrete tubercles (Fig. 10A). This bone resembles the AL of *Williamsaspis*, and other primitive arthrodires (e.g., *Simblaspis*, *Aethaspis*; see Denison, 1958:fig. 110; White, 1969:figs. 2–10), in the absence of a projecting posteroventral corner and in the development of the 'apron' (postbranchial lamina). ANU V1025 differs from the restoration of the AL of *Williamsaspis* by White (1952:fig. 7) in the low rounded anterodorsal corner and the configuration of the dorsal margin. However, this region in the holotype is represented only by an internal impression of the contact face for the ADL, which could have been more prominent than restored by White. The concentric linear ornament of ANU V1025 and the distinct horizontal ridge crossing the plate from the ossification center to the posterior corner are clear resemblances to the corresponding bone in *Williamsaspis*. The ADL illustrated in Figure 10B has an overlap for the AL corresponding closely in size and shape to the clearly impressed contact face for the ADL on the inner surface of V1025. On this evidence, we consider that both of these bones, and the ADL described by Long (1984b) as *Errolosteus* cf. *E. goodradigbeensis*, probably belong to a new form of williamsaspid.

As noted above, ridged ornament occurs in other brachythoracids (e.g., *Holonema*) and phlyctaenioids (e.g., *Williamsaspis*) and is also characteristic of certain taxa within other placoderm groups (e.g., petalichthyids, antiarchs). In particular, ornament of the Chinese Middle Devonian antiarch *Hunanolepis* is remarkably similar to that described here for *Uralosteus* (e.g., Wang, 1991:pls. 2, 4), the observable differences being the less crowded tubercles on the ridges and some wide tuberculated zones without ridges (Wang, 1991:pl. 3). There are also other isolated arthrodire bones from the Emsian limestones of southeastern Australia that have ridged ornament, but evidently do not belong to *Errolosteus goodradigbeensis* or *Uralosteus* (see below).

RELATIONSHIPS

Brachythoracid arthrodires were one of the most diverse and successful groups of early gnathostome fishes (e.g., Young, 1986; Janvier, 1996), particularly in marine environments during the Late Devonian (e.g., Carr, 1995) where they included probably the largest predators of their time. However, the key to understanding the interrelationships of the major brachythoracid subgroups is in the analysis of more primitive taxa known from the Early and early Middle Devonian. The major regions of the world contributing information on primitive brachythoracids are the classic localities in the Baltic area (*Homostius*, e.g., Heintz, 1934; Mark, 1963; Mark-Kurik, 1992, 1993; *Heterostius* Heintz, 1930), the Early Devonian of the Rhineland (e.g., *Tityosteus*; Gross, 1960; Otto, 1992), the Emsian of Morocco (Lelièvre, 1984a, b, 1988, 1995) and southeastern Australia ('buchanosteid' arthrodires and related forms; White, 1952, 1978; White and Toombs, 1972; Young, 1979, 1981; Long, 1984a, b; Findlay, 1996).

The genus *Buchanosteus* was erected by Stensiö (1945) for an isolated skull of which endocranial structures had been earlier described by Hills (1936). White and Toombs (1972) referred remains from Burrinjuck to a new genus, '*Parabuchanosteus murrumbidgeensis*', but Young (1979) argued that all their described material could be referred to the type species, *Buchanosteus confertituberculatus* (Chapman). Long (1991) referred an articulated trunk armor from Buchan to '*Buchanosteus*', and 'buchanosteid' scales illustrated by Burrow and Turner (1998) came from this specimen (see above), of which the skull is unknown. Findlay (1996:167) supported the genus *Parabuchanosteus*, noting possible differences in the form of myodomes in the orbit of a new specimen with the same parasphenoid shape as described for *Parabuchanosteus*. It seems now that there was a complex of similar small to medium 'buchanosteid' arthrodires which resembled each other in shared primitive features, but had varying phylogenetic relationships to higher brachythoracids (see Young et al., 2001).

'Buchanosteids' have featured in several recent analyses of brachythoracid interrelationships (e.g., Lelièvre, 1988, 1995; Gardiner, 1990; Carr, 1991; Johnson and Elliott, 1995), but the fact that most taxa are based on disarticulated specimens requires caution in accepting certain character combinations. For example, White (1978:162) referred an AMV plate with overlap areas for AV plates to *Buchanosteus*, but if correct this would be the only brachythoracid (and phlyctaenioid) to possess the AV plate, so we consider this assignment to be incorrect. Findlay (1996) referred an isolated PNu plate to *Errolosteus* on its similar ridged ornament to the holotype, but suggested that it possessed a sliding dermal neck joint, which would place *Errolosteus* outside the phlyctaenioids. However, the posterior position of the branching points for the pitlines adjacent to the endolymphatic opening is diagnostic of phlyctaenioids (Goujet, 1984), and we interpret this specimen to be incomplete, with the articular fossa for the neck joint lost by abrasion.

Specimens in which various skull and trunk armor bones are associated, such as *Uralosteus bashkiricus* described above, have special importance in establishing character associations for phylogenetic studies. Young (1981:fig. 17) provisionally grouped three genera from Burrinjuck (*Burrinjucosteus*, *Toombsosteus*, *Errolosteus*) in an unresolved trichotomy using two characters as synapomorphies (broad, depressed body shape; overlap area along ventral margin of AL). Since neither specimen of the AL of *Uralosteus bashkiricus* has the ventral margin preserved, the status of the second character remains unknown (only a contact face for the SP plate is preserved, the normal condition). This clade was placed by Young (1981) in an unresolved trichotomy with two other primitive brachythoracids from Burrinjuck (*Buchanosteus*, *Arenipiscis*), which showed a general resemblance in a range of primitive features. The genus *Goodradigbeeon* White, 1978 was interpreted as more primitive because it lacked three features possessed by the other taxa (SO plate with a slender suborbital lamina, reduced lateral trunk-shield wall, supragnathals with posterior processes).

Lelièvre (1988) suggested a relationship between *Errolosteus* and *Buchanosteus* based on three characters (1, 5, 18 on his fig. 4), but one (sensory canals on SO plate) was wrongly coded (not known in *Errolosteus*), and the other two characters are generalised primitive features. Lelièvre (1995) developed his phylogenetic analysis of primitive brachythoracids with a data matrix of 53 characters, the following characters defining his major groupings:

Synapomorphies defining the Brachythoraci:

1. Skull roof bones with extensive overlaps
2. Posterior postorbital process with only one branch
6. Postnuchal process on paranuchal plate

Synapomorphies defining the Migmatocephala:

11. Elongate nuchal and paranuchal plates
38. MD plate shorter than broad

Synapomorphies defining the Eubrachythoraci:

16. PrO plate forming an embayment of the central plate
30. Occlusal surface of anterior supragnathal smooth, rather than denticulate
47. Separated supraoral and infraorbital sensory lines on suborbital plate
48. Occipital cross-commissure passing behind nuchal onto extrascapulars, or absent

However, of these main characters, only three (1, 6, 38) can be determined for *Uralosteus bashkiricus*, and our initial assumption that ornament similarities indicate a close relationship between *Uralosteus* and *Errolosteus goodradigbeensis* is difficult to test because of incomplete data from both taxa. *Errolosteus* was one of 17 genera excluded from analysis by Lelièvre (1995:194) because more than 50% of the 53 characters in his data matrix could not be coded; the same applies to *Uralosteus*.

One interesting character of *Uralosteus*, the unusual arrangement of the PL overlapping the ADL, was first described by White and Toombs (1972:pl. 7, fig. 2), as a defining characteristic of the family Buchanosteidae. It was included in the family diagnosis of Young (1979:345), and as noted above was used by Mark-Kurik (1991:fig. 3F) to assign an ADL from the Emsian of Severnaya Zemlya to the Buchanosteidae. In typical arthrodires the ADL overlaps the PL (e.g., Miles and Westoll, 1968:fig. 35). The only previous record of this feature is the arthrodire *Arctonema*, based on an isolated incomplete ADL from Spitsbergen. This clearly shows the second overlap (Ørvig, 1969b:fig. 1A) even though it was not mentioned in Ørvig's description, nor completely included in his restoration (1969b:fig. 2A). Assuming that this is a specialized rather than primitive character, we can consider *Arctonema* to be a buchanosteid, as previously suggested (Mark-Kurik, 1991:19). As noted above, another specimen from Buchan, Victoria, attributed to *Buchanosteus* by Long (1984a, 1991), does not show this feature, and its ADL shape and sensory canal pattern are more suggestive of *Coccosteus* (e.g., Miles and Westoll, 1968). The armor restoration of '*Parabuchanosteus*' proposed by White and Toombs (1972:fig. 24) and the specimen figured by Long both had a pectoral fenestra, whereas the high narrow AL of *Uralosteus* suggests a pectoral embayment (Fig. 7B), making it more advanced in this respect than *Coccosteus* (e.g., Miles, 1969). This would indicate independent loss of the pectoral fenestra if a monophyletic grouping of *Uralosteus* and *Errolosteus* is supported by characters additional to the distinctive ridged ornament. Significant morphological aspects, unknown in the holotype of *Uralosteus* and therefore dependent on the discovery of new material, include the dermal bone pattern of the anterior part of the skull (with either a T-shaped rostral plate as in eubrachythoracids, or with a rostral capsule and persistent orbital fissure as in *Errolosteus*). For *Errolosteus* the trunk armor and cheek are very poorly known, and features of the (unknown) MD plate would provide a ready indication of the likely close relationship with *Uralosteus*, which has a distinctive MD plate.

In summary, the new taxon *Uralosteus bashkiricus* described above from the Emsian of the Ural Mountains is significant in the association of vertebrate microremains with skull and trunk armor bones. The macroremains permit its approximate placement in a phylogenetic scheme as a primitive brachythoracid belonging to the Buchanosteidae as defined above. Although poorly understood, the highly distinctive dermal ornament of *Uralosteus bashkiricus* should facilitate the recognition of additional material. New specimens are needed to elucidate its detailed relationship to similar forms (*Errolosteus* from the Emsian of East Gondwana). Finally, this new discovery adds to the wide distribution for the family Buchanosteidae, which was already extended from the type area of southeastern Australia with finds in Europe and Russia (Mark-Kurik, 1991), China (e.g., Young and Janvier, 1999) and the Middle East (Lelièvre et al., 1994; Young et al., 2001). Discoveries so far indicate that the group was restricted to shallow marine environments of Emsian age across the eastern and northern margins of Gondwana, and through the Uralian seaway to Spitsbergen, Severnaya Zemlya and other areas, all regions that were positioned in low latitudes during Early Devonian time (Young et al., 2000; Young, 2003).

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