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A new, giant xiphosurid from the lower Namurian of Weardale, County Durham

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SUMMARY: One of the largest xiphosurid specimens known from the fossil record, found in the lower Namurian strata of Weardale, is described as *Xaniopyramis linseyi* gen. et sp. nov. It is referred to the Limuloidea, Moravuridae Přibyl, 1967. *Xaniopyramis* was probably a burrowing form and a poor swimmer; it is the first xiphosurid body fossil recorded from the British Namurian and supports the idea of a marine faunal connection at this time with the central-eastern European area.

While undertaking an undergraduate field mapping project (University of Hull) in Carboniferous strata on the south side of Weardale during the summer of 1983, T. K. Linsey discovered a single, very large xiphosurid specimen. In general, xiphosurids occur rather sporadically in the fossil record, from the Cambrian onwards, and they have been cited by various authors as a morphologically conservative group throughout much of their stratigraphic range. When they do occur, individual specimens are often sufficiently distinct to form the basis of a new taxon or taxa of at least generic rank. The Weardale xiphosurid falls into this pattern.

This fossil is important in several respects. Firstly, it represents a new genus, *Xaniopyramis*, of the Moravuridae Přibyl, 1967, there being just one other known specimen of this family. Secondly, the only limuloid older than *Xaniopyramis* is the slightly earlier *Rolfeia* Waterston, 1985 from the Tournaisian of Berwickshire, Scotland. *Moravurus rehori* Přibyl, 1967, from Czechoslavakia, is about the same age as the Weardale form, to which it is most closely related. Thirdly, amongst fossil xiphosurids it seems that only *Tachypleus decheni* (Zincken, 1862) (see Böhm 1905) from the German Miocene is larger. The xiphosurid status of *Kiaeria* Størmer, 1934 from the 'Downton' Old Red Sandstone facies of the Ringerike area. Norway (of Přidolí and in part Ludlow, late Silurian age; see Worsley *et al.* 1982), and of '*Limulus*' *nathorsti* Jackson, 1906 from the Jurassic of Sweden, the material of both of which is bigger than our specimen, is in our opinion debatable. Discussion of the phylogenetic implications of *Xaniopyramis* will be presented in a forthcoming paper (Selden & Siveter in preparation). The Weardale specimen is the first xiphosurid body fossil known from the British Namurian; palaeogeographically it supports the notion of faunal migrations between Britain and the central-eastern European area at this time.

The specimen is deposited in the type and figured collections of the Geology Department, University of Hull (HU.)

1. OCCURRENCE

1.1. Locality

The specimen was found in a loose block of sandstone in a stream bed at a height of 540m on the northern side of Noon Hill, towards the headwaters of a small unnamed tributary that runs parallel with Ireshope Burn, about 2.5km SSW of Ireshopeburn village [NY 8526 3659] (Fig. 1). It may have been dislodged during several days of heavy rain preceeding the discovery, which had caused the ubiquitious peat cover to slip. Only the external mould is known, the counterpart has unfortunately not been located, despite a return visit by us.

1.2. Geological horizon

In the Weardale area, which is situated on the Alston Block, Namurian sandstones are typical, and it is undoubtedly from one of these that the fossil-bearing slab came. The northern slopes of Noon Hill, the bedrock of which it is assumed provided the sandstone slab, are formed of strata between the Great Limestone and unnamed sediments just above the top of the Upper Fell Top Limestone. All these beds belong to the Upper Limestone Group as shown on the British Geological Survey Alston map (one inch to one mile, sheet 25), which are of lower Namurian, Pendleian to lower Arnsbergian age (Fig. 2). It has not been possible to corroborate the age of the fossil by independent palaeontological data; no other macrofossils are present on the slab, and an attempt (by Dr B. Owens) to recover palynological specimens has proved fruitless.

Topographically the locality is some 50m above the top of the Firestone Sill and, because the beds dip gently, this figure also approximates to a stratigraphic height above the same unit. The authors are not aware of any published detailed section of the Noon Hill – Ireshope Burn area, but with respect to the lithostratigraphic divisions present on the Alston map, the locality would be placed within about 120m of strata that are

termed in the legend 'mainly mudstones' (Fig. 3). We found some sandstone horizons within this poorly exposed 'mainly mudstone' sequence in the stream from which specimens came, and several metres above the spot where the xiphosurid was found there was a shell bed comprising mainly decalcified crinoid ossicles with comminuted brachiopods. Comparing the Noon Hill – Ireshope Burn sequence with the nearby Greenlaws – Swinhope section, 3 to 5 km away to the east, the xiphosurid level would seem to correlate with a horizon between the Crag Limestone and the base of the Harthope Ganister. These beds are of upper E_1 to lower E_2 age and are within the Nl mesothem of Ramsbottom (see Figs 2, 3 and Ramsbottom 1977, table 1, fig. 4). More particularly, the stratigraphic height of the xiphosurid level above the Firestone Sill loosely approximates to that of the Lower and Upper Rookhope Shell beds mapped out elsewhere on the Alston Block, these being calcareous fine-grained sandstones that typically contain crinoid and brachiopod debris (Dr. C. J. Percival, pers. comm. 28.11.85). The xiphosurid level is thus probably of Pendleian (E_1) age.

2. TERMINOLOGY

The terms employed by Størmer (1955) to describe merostomes and the amendments of Ambrose & Romano (1972) have mostly been used by us, but a few modifications and one new term are introduced herein to accommodate the distinctive morphology of the Moravuridae. The reader is referred to the explanatory diagrams of these authors, with the following modifications. The term posteromarginal facet, coined by Pickett (1984, p.614, after Meischner 1962), has been adopted and in common with that author we also use the term free lobe (= opercular pleurite or elevated opercular pleurite of other workers, for example Eldredge 1970, Fisher 1981 and Waterston 1985). The posteromarginal facet also corresponds to the abaxial part of what some authors (Fisher 1981, p. 55, fig. 2;

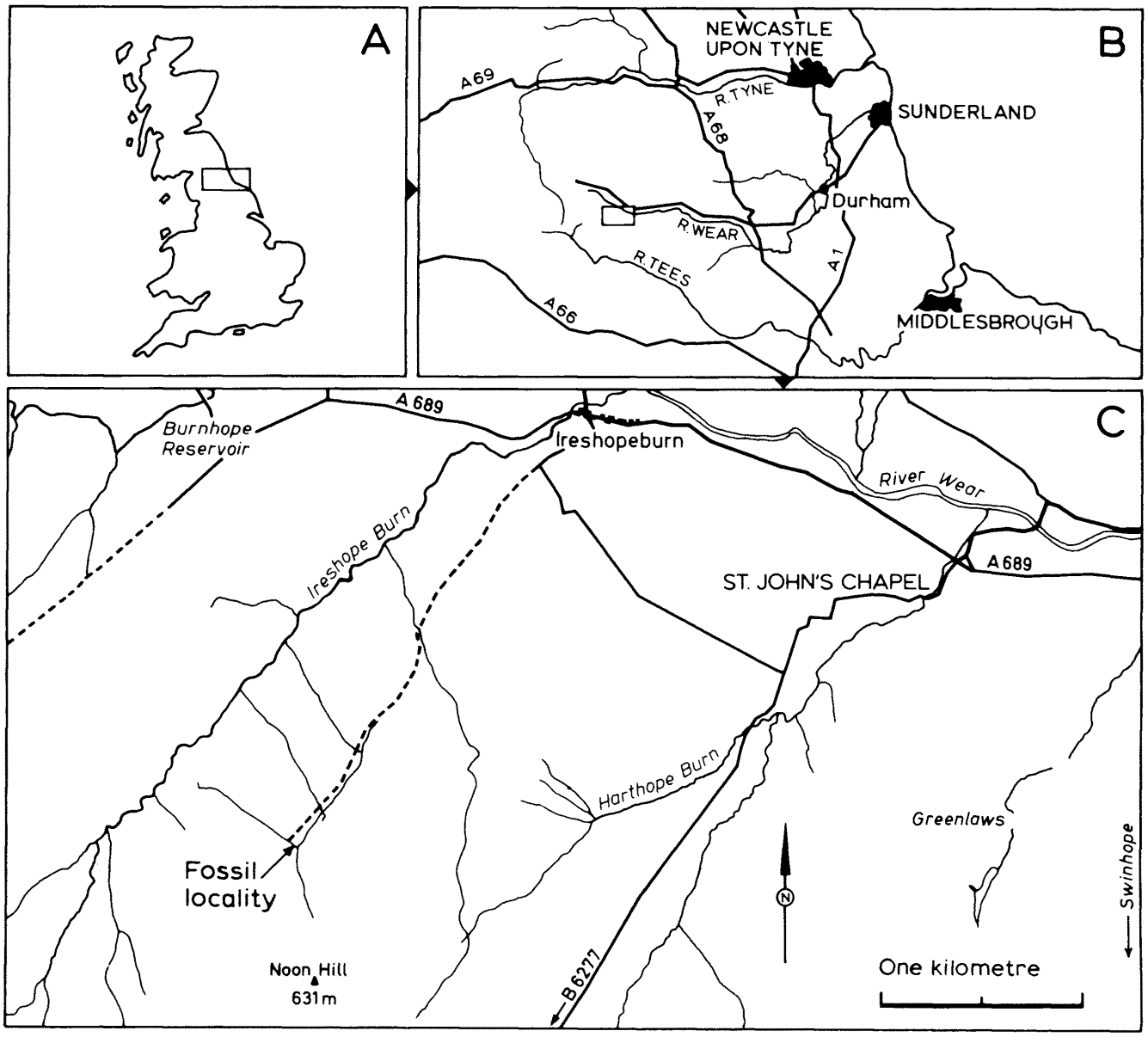

Fig. 1. Locality map.

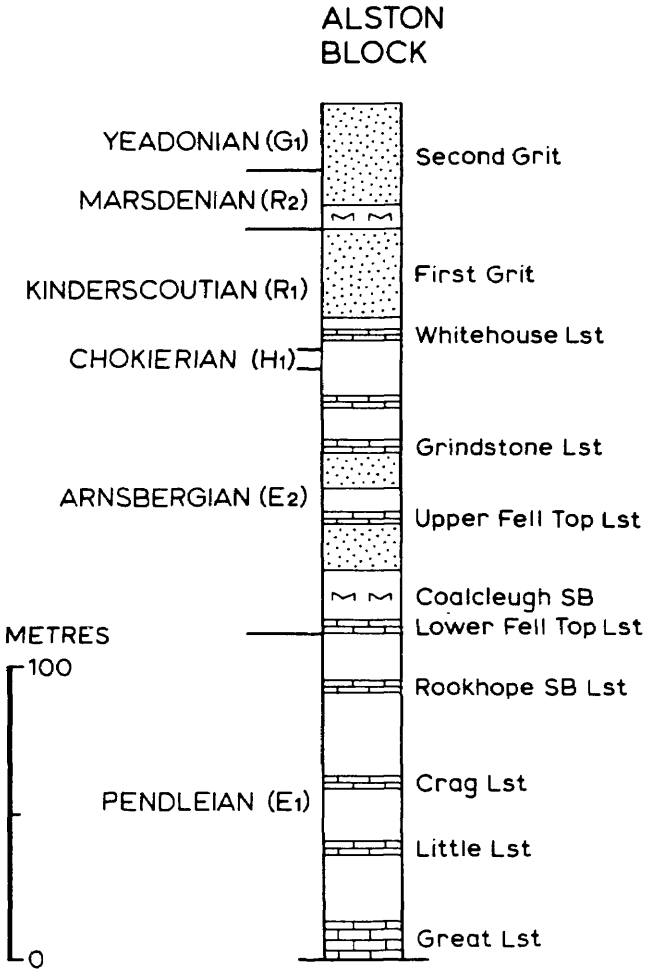

Fig. 2. Namurian succession, Alston Block. After Ramsbottom *et al.* 1978, fig. 9, section D.

Waterston 1985) have termed the occipital band.

The prosoma (= cephalothorax) is the foremost body tagma in the Chelicerata (van der Hammen 1985; Selden 1981) and not merely the dorsal shield (cf. Størmer 1955), which is termed the carapace. Similarly, the opisthosoma (= abdomen) describes the posterior tagma, and we use the term thoracetron (see Raymond 1944, p. 476) to describe the fully fused dorsal shield of the opisthosoma in the Limuloidea and Euproopoidea.

The term pleural ridge as employed by Ambrose and Romano (1972, p. 570; cf. Eller 1938a, p. 130) has been qualified by us to include transverse and longitudinal types, the former equating with the ridges on the thoracetron separating the pleural ribs, the latter crossing both the transverse pleural ridges and pleural ribs on the thoracetron at approximately right angles. We introduce the term cheek ridge for that ridge running forwards on the carapace from the obtusely angled junction of the two ridges which form the anterior boundary of the posteromarginal facet (Fig. 5). The spelling of *Bellinurus* Pictet, 1846 and derivatives is used in agreement with Morris (1980, p. 31).

3. PRESERVATION AND MORPHOLOGICAL RECONSTRUCTION

3.1. Preservation

The external mould is preserved on the bedding surface of a 4.5cm-thick sandstone. Almost all the mould is smeared with a thin mineral film, identified by energy dispersive spectrometry analysis as consisting dominantly of iron and manganese salts. This film effectively masks any original surface detail and it obscures the exact nature of the prosoma–opisthosoma boundary, together with the point of origin of the probable free lobe. The mould of the right genal spine, the two preserved marginal spines on the right side of the opisthosoma, the one preserved small, broadly-based spine on the posteriorly projected longitudinal pleural ridge, together with one large and several small irregular patches on the prosoma, lack this iron-manganese coating. Sediment covers posterior and outer parts of the opisthosoma, and the left genal area and telson are missing.

A silicone rubber cast of the external mould gives a clearer indication of its morphology (Figs 4-6). The prosoma has suffered oblique-vertical compaction and distortion from left to right, so that on the left side the taxonomically diagnostic ridged, pyramidal structure (see below) is but weakly indicated. Such distortion would also account for the offsetting to the right of the cardiac lobe relative to the cardiac ridge, and perhaps also, at least to some extent, for the very close juxtaposition of the muscle impressions and the

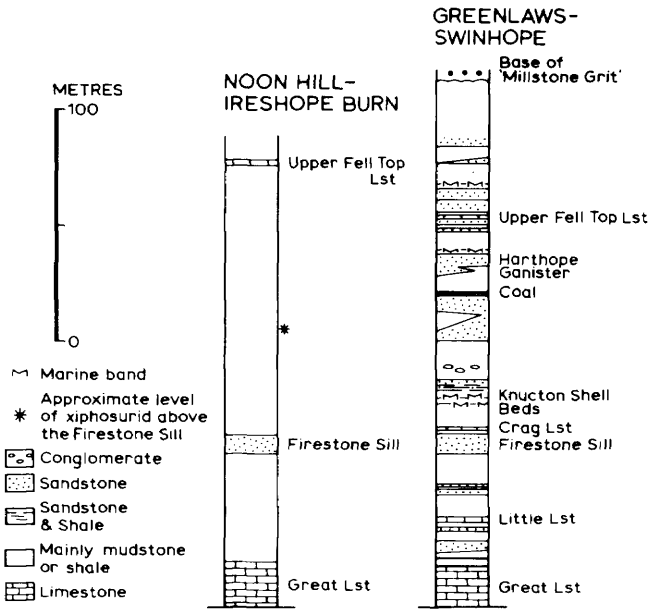

Fig. 3. Lithostratigraphy above the Great Limestone, Namurian Series, southern side of Weardale in the vicinity of St. John's Chapel. Greenlaws succession taken from Dunham 1949, fig. 4, section 5; based on Greenlaws Mine workings and exposure in Swinhope. Noon Hill – Ireshope Burn succession constructed from strata represented on the British Geological Survey Alston map, Sheet No. 25, 1" to 1 mile.

ophthalmic ridge to the right of the cardiac lobe. All the cardiophthalmic region is below the height of the ophthalmic ridge, another feature that is likely to have resulted from compaction. In the left cheek area the prosoma seems to have responded to compaction by a folding or wrinkling, rather than a fracturing, of the cuticle.

Around much of the prosoma there is a skewed, crescentic mark on the sediment surface which it is thought was formed by current scour (see section 6.2).

3.2. Morphological reconstruction

A suggested reconstruction is given in Figure 7.

The prosoma–opisthosoma hinge is poorly known in *Xaniopyramis* yet the form and function of this joint and the positions of the cardiac and axial furrows were considered characters of fundamental significance in xiphosurid evolution by Eldredge (1974, p. 35). Amongst bellinuroids some taxa have, like the Limuloidea and the Euproopoidea, the axial furrows of the opisthosoma aligned with the cardiac furrows of the prosoma; this produces a strong articulation necessary for strong flexion between these tagmata. Bellinuroids with this form of articulation include the late Devonian *Neobelinuropsis* Eller, 1938a and some species of *Bellinurus*. Other bellinuroids exhibit the more primitive articulation in which the axial furrows are aligned with the ophthalmic ridges, a condition shown also by the Synziphosurina and the Pseudoniscina. Since

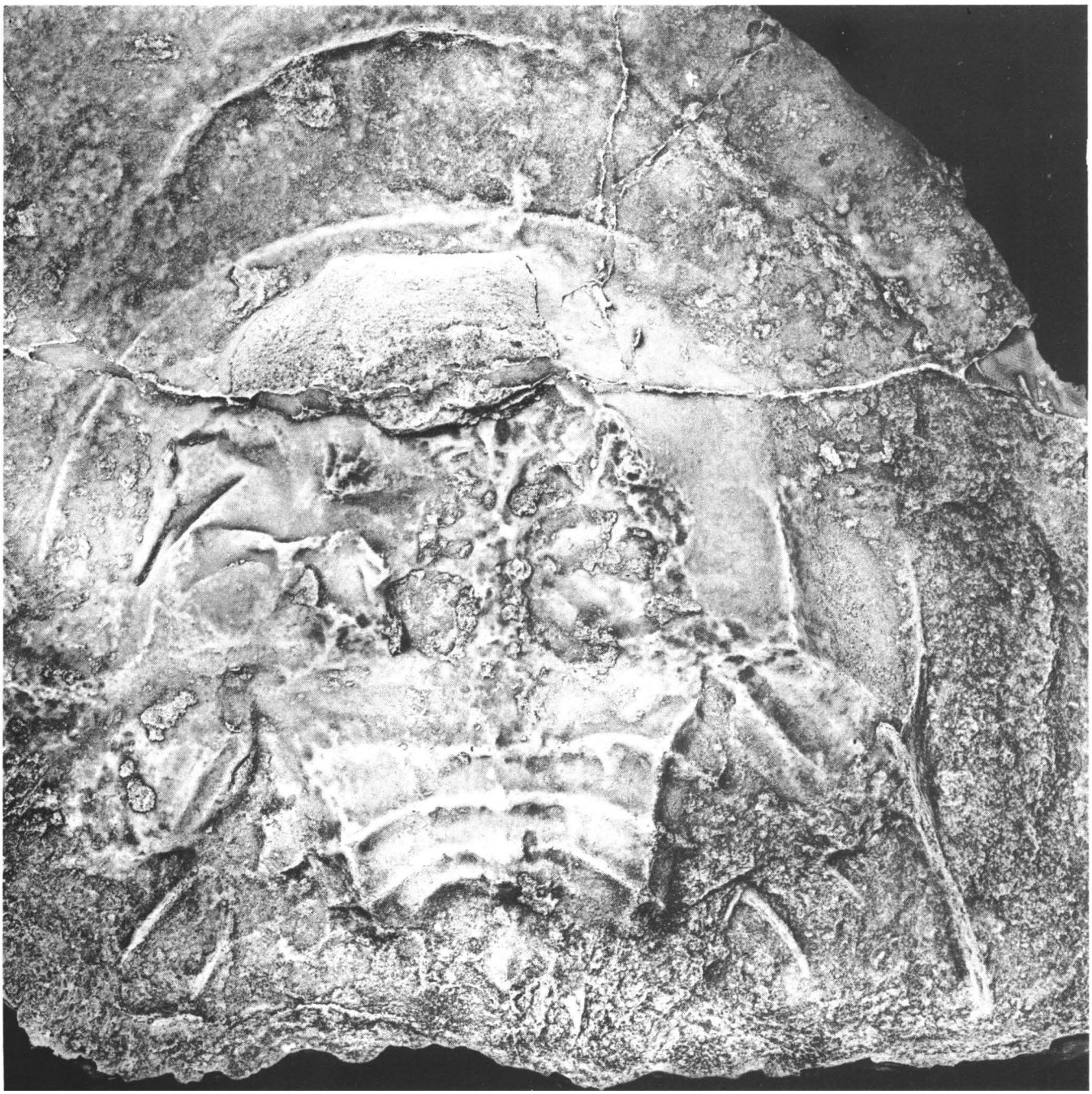

Fig. 4. *Xaniopyramis linseyi* gen. et sp. nov. Silicone rubber cast of holotype, HU P1986.1, lower Namurian, Weardale, County Durham; dorsal view, ×1.

only the narrower articulation occurs in the Limuloidea, it can be reasonably assumed that *Xaniopyramis* has this articulation type, as it is undoubtedly a limuloid. The position of the hinge-line is uncertain, and is reconstructed by interpolation as a transverse line between the lateral, better preserved parts. The gentle curve of the ophthalmic ridge is extrapolated backwards, on both sides, to meet the inferred hinge-line at right angles. Only the posterior half of the first visible opisthosomal segment can be seen, but the presence of an axial node on this segment, the long (right) longitudinal pleural ridge associated with the segment and extrapolation of its length as probably being the longest of the opisthosoma (since they become progressively shorter posteriorly) suggest that it takes up most of the area up to the position of the presumed hinge-line. Furthermore, if our interpretation of the oval areas anterolaterally on the opisthosoma as free lobes is correct (see below), then the axial and pleural portions between the longitudinal ridges of the segment

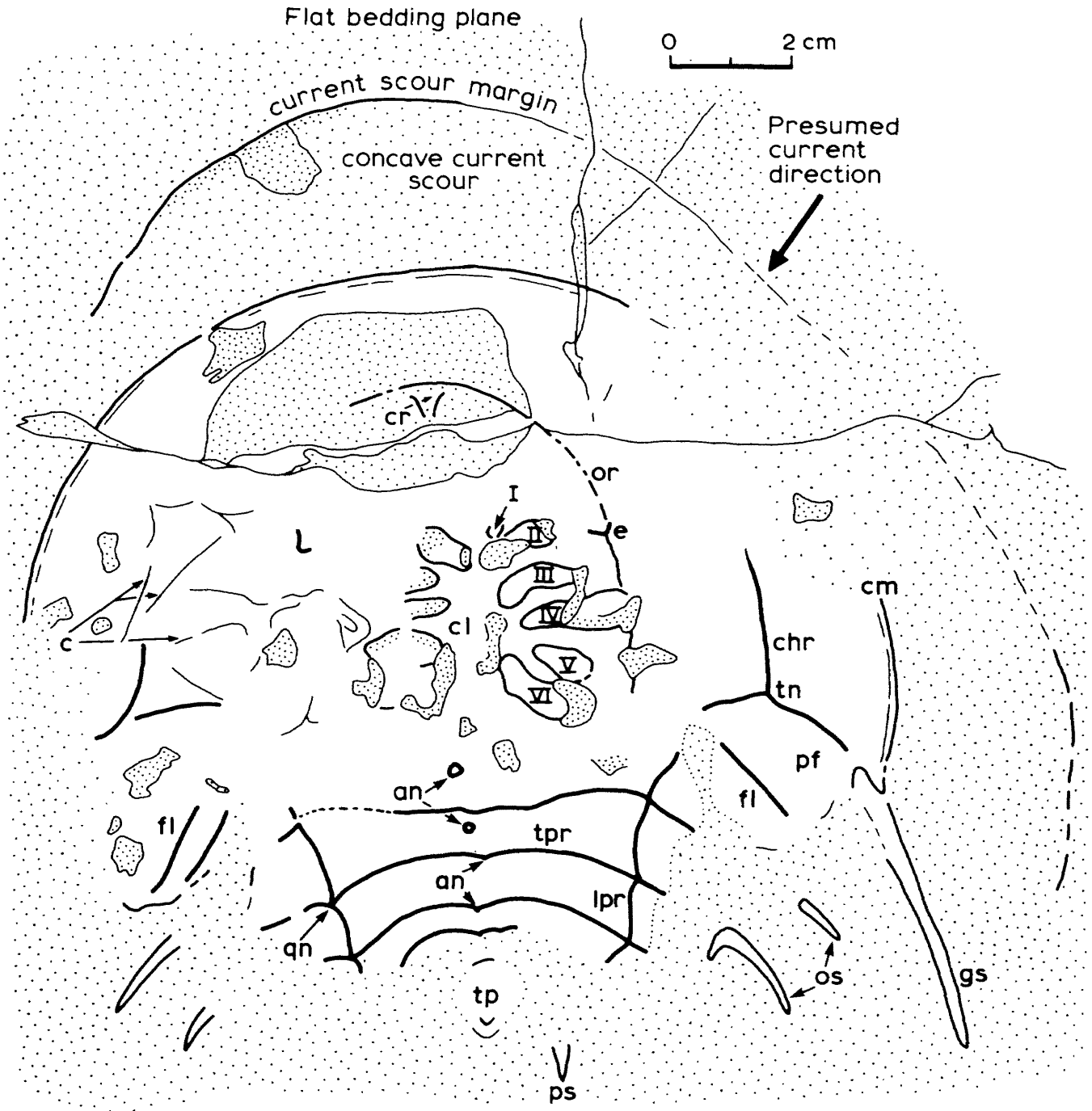

Fig. 5. *Xaniopyramis linseyi* gen. et sp. nov. Explanatory camera lucida diagram, based on Fig. 4, holotype, HU P1986.1, lower Namurian, Weardale, County Durham; dorsal view, ×1. an=axial node, c=compaction creases in cuticle, chr=cheek ridge, cl=cardiac lobe, cm=carapace margin, cr=cardiac ridge, e=eye, fl=free lobe, gs=genal spine, lpr=longitudinal pleural ridge, or=ophthalmic ridge, os=opisthosomal spine, pf=posteromarginal facet, ps=posterior spine, qn=quadriradiate node, tn=triradiate node, tp=terminal piece of axis, tpr=transverse pleural ridge, I=chelicera muscle impression, II to VI=walking legs muscle impressions.

preceding the first long one must be reduced or absorbed into the prosoma, at least for the most part, since the anterior part of, if not all of, the free lobe would be homologous with the lateral pleural parts of the segment (Selden & Siveter in preparation).

Only the right genal spine is preserved. It is long and does not follow the curve of the carapace edge but is deflected abaxially. The base of the spine appears to have broken off from the genal area and to lie above the posteromarginal facet, and the spine to have moved relative to the carapace. We have restored the spine to its presumed life position.

The most enigmatic region is the anterolateral corner of the thoracetron and the posterolateral area of the carapace. Posterior to the posteromarginal facet is an oval area which bears a prominent median ridge along its long axis. On either side of this ridge the oval area slopes gently downwards. The anterior edge of the oval area is poorly defined on the right side but is more distinct on the left. The posterior border of the oval area is more distinct and on both sides of the specimen a tongue of matrix fills the depression between it and the thoracetron. Additionally, on the left oval area, a straight ridge, paralleling the median ridge, occurs adjacent to the posterior border, and the area posterior to this ridge descends steeply into the matrix. This feature is not so apparent on the right oval area. The problematic oval structure is best interpreted by comparing it with similar structures in other limuloids, and by functional considerations. Comparison with the Permian *Paleolimulus avitus* Dunbar, 1923 (see Raymond 1944, p. 505) and later limuloids suggests that the oval area is a free lobe (option 1, Fig. 7A). A second option (Fig. 7B) is that the oval area is part of the carapace: the posteromarginal facet vastly expanded into a flange.

Option 1 for the oval structure is intuitively more attractive than option 2, since a comparable structure is known in other xiphosurid genera, whereas a carapace flange is not. A more distinct anterior margin to the oval area would be expected if option 1 were correct, though the mineralized coating on the surface of the fossil (see section 3.1) would have obscured such a margin, if originally present. Consideration of functional morphology and evolution of free lobes in *Xaniopyramis* and other xiphosurids (section 5 and Selden & Siveter in preparation) renders option 1 the most plausible.

The cardiophthalmic region and the opthalmic ridge on the left side were both affected by compaction (section 3.1); in the reconstruction these features have been restored to their presumed original appearance. On either side of and gently radiating from the cardiac lobe there are five pairs of lobate depressions. These are believed to represent attachment impressions of plastrotergal muscles associated with prosomal appendages II to VI. Additionally, on the right side, a

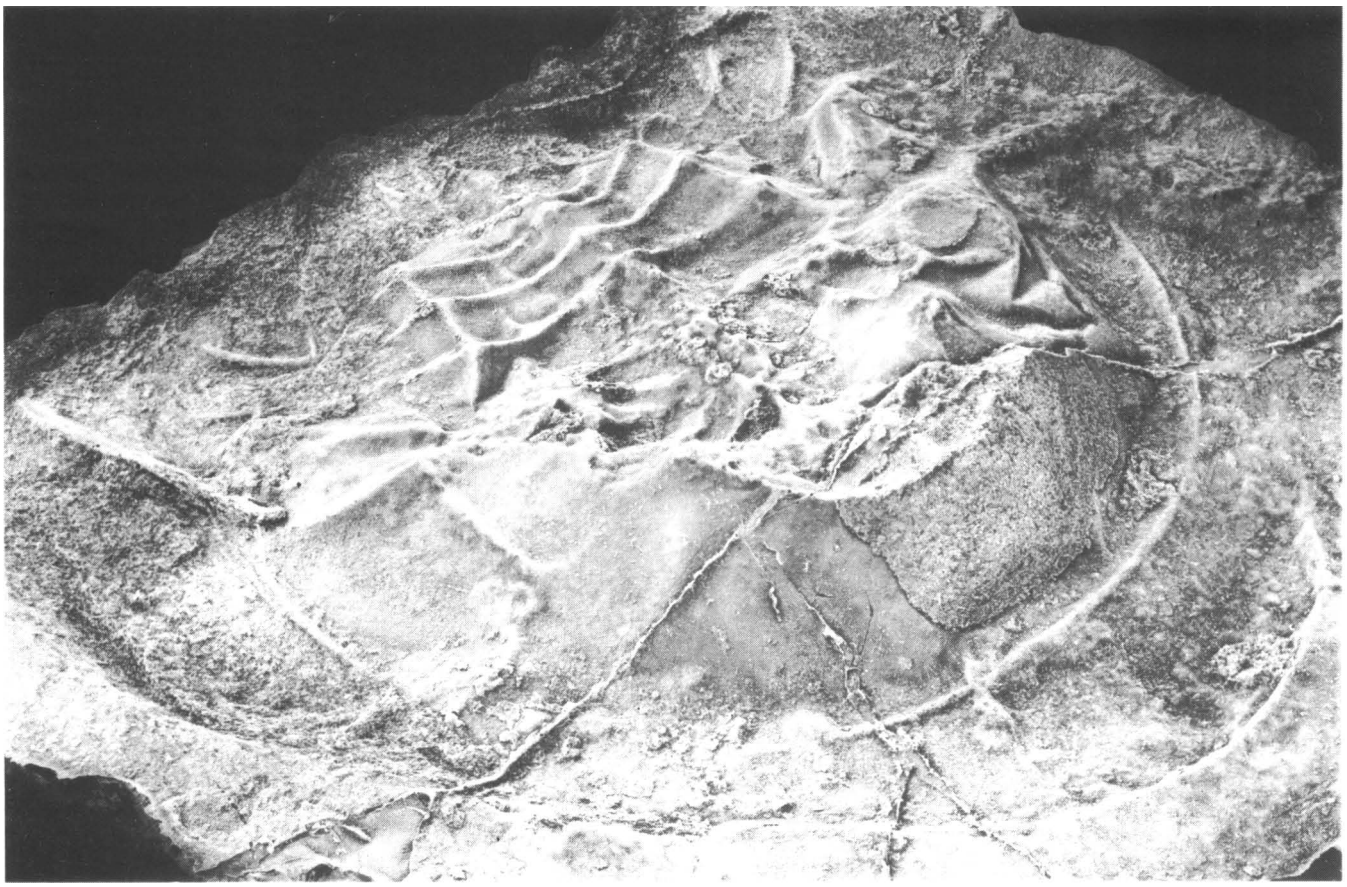

Fig. 6. *Xaniopyramis linseyi* gen. et sp. nov. Silicone rubber cast of holotype, HU P1986.1, lower Namurian, Weardale, County Durham; oblique view, × 0.9.

small muscle impression is preserved (I), presumably of the chelicera; this too would have been paired in life.

The lateral spines of the opisthosoma are gently curved, tapering to a point and appear robust, suggesting a circular cross-section; at least one base appears distinct and bulbous (see species description) and in general the spines appear much more like movable spines than mere flat thoracetron flanges. The lateral margins of the thoracetron are not preserved, but a gently fluted outline may be supposed on the basis of the disposition of the bases of the movable spines combined with the shape of the thoracetron surface as it approaches the margin; the latter is revealed by the scalloped edge to the overlying matrix on the right side of the specimen (Fig. 5). The numbers of movable spines and flutes on the thoracetron margin are uncertain.

The posterior part of the opisthosoma is very poorly preserved and much of this region, including the telson, is reconstructed by comparison with other limuloids and bearing in mind functional considerations (see section 5). At the posterior end of the opisthosomal axis is a diamond-shaped raised area with a broad median node (tp, Fig. 5). This is comparable with the diamond-shaped feature with an elongate median node in *Moravurus* Přibyl, 1967 (pl. 1, fig. 2) and the raised axial portion of the posterior part of the thoracetron of *Paleolimulus* Dunbar, 1923 (pl. 2, fig. 1). This feature of *Paleolimulus* is flanked on either side, at a short distance, by a posteriorly-directed, flattened spine-like ridge forming the posterior termination of the longitudinal pleural ridge of the thoracetron. Similarly, the flattened spine to the right of the axial diamond-shaped structure of *Xaniopyramis* is considered to represent the posterior termination of the right longitudinal ridge, rather than the posterior spinose termination of the thoracetron. A long telson has been assumed on the basis of functional considerations (see section 5.1).

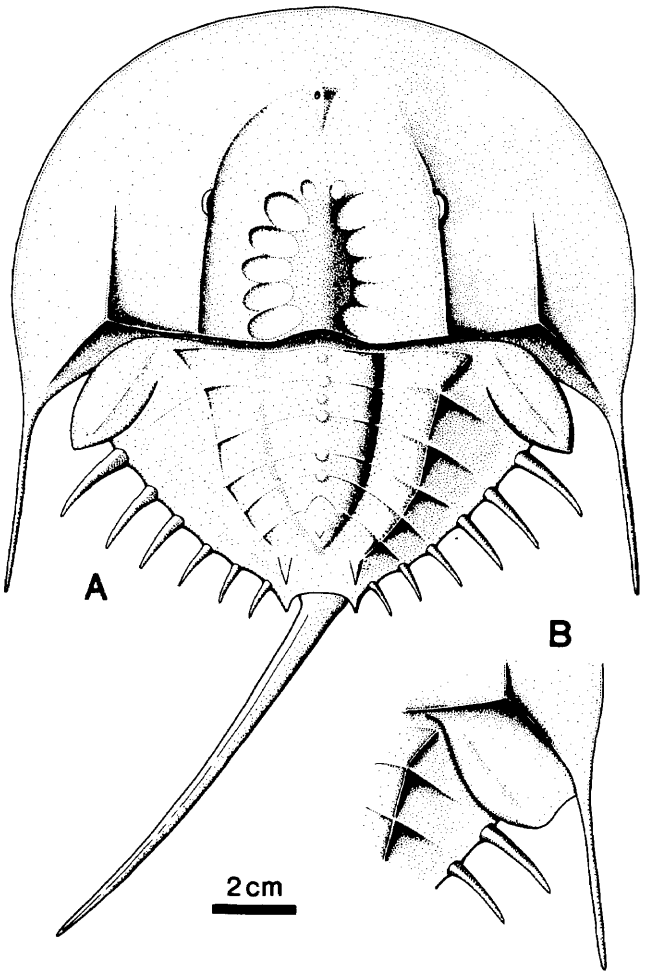

Fig. 7. Reconstruction of *Xaniopyramis linseyi* gen. et sp. nov. based on holotype.
A. Dorsal view of whole animal as reconstructed with free lobe on thoracetron (option 1).
B. Alternative reconstruction; corner of thoracetron without free lobe, plus posterolateral corner of carapace, the posteromarginal facet of which has an extended flange (option 2).

4. SYSTEMATIC PALAEONTOLOGY

Phylum CHELICERATA Heymons, 1901
Class XIPHOSURA Latreille, 1802
Order XIPHOSURIDA Latreille, 1802
Suborder LIMULINA Richter & Richter, 1929
Infraorder LIMULICINA Richter & Richter, 1929
Superfamily LIMULOIDEA Zittel, 1885

Discussion. The classification followed herein is essentially that of Eldredge (1974), although modification of this scheme will be necessary in the light of Fisher's (1981, 1982, 1984) phylogenetic analyses. Members of the Limuloidea and the Euproopoidea have a thoracetron and are thus distinguished from members of the Bellinuroidea which have free opisthosomal tergites. Features of the Moravuridae that are typical of the Limuloidea are: the possession of a dorsal posteromarginal facet on the prosoma, movable opisthosomal spines (in *Xaniopyramis*), ophthalmic ridges which are parallel behind the eyes (see Størmer 1955) and which are not posteriorly extended (as in euroopoids) into spines, and a free lobe on the opisthosoma. These characters do not occur in the Euproopoidea, to which superfamily Přibyl (1967, p. 457) originally assigned his new family though admittedly without the information at his disposal that we now have from *Xaniopyramis*.

Family MORAVURIDAE Přibyl, 1967

Type genus. Moravurus Přibyl, 1967; Carboniferous, basal part of the Namurian Series, E_1 Zone, upper part of the Kyjovice Formation, Štúr marine band, Tichá near Frenštát, Ostrava-Kariná district, Moravia, Czechoslovakia. By monotypy.

Other genera. Xaniopyramis gen. nov.

Diagnosis. Limuloids with both transverse and longitudinal pleural ridges on the thoracetron, a

quadriradiate node marking each intersection point, of which there are at least three on each pleural area, of these ridges. Axis has six segments and at least four axial ridges each with a median node. (Modified from Přibyl 1967, p. 457).

Discussion. The Moravuridae and *Moravurus,* type species *M. rehori,* were established solely on the basis of a single distinctive thoracetron; this exhibits a pattern of intersecting transverse and longitudinal pleural ridges and nodes, and axial ridges and nodes, which are unique within the Xiphosurida. *Xaniopyramis* exhibits a similar comparable, though different, network of pleural ridges and nodes (see generic discussion), and is about the same age as *Moravurus;* it undoubtedly fits into the Moravuridae. The triradiate ridge on the carapace, as shown by *Xaniopyramis,* might also in time be recognised as a diagnostic family character.

Of the other limuloid families, which were recently discussed by Pickett (1984), the Australian Triassic Austrolimulidae Riek, 1955 and Dubbolimulidae Pickett, 1984 both contain just a single, highly individual genus and are easily differentiated from the Moravuridae. None of the genera now included in the Limulidae Zittel, 1885, (that is *Mesolimulus* Størmer, 1952; *Psammolimulus* Lange, 1923; *Victalimulus* Riek & Gill, 1971; *Heterolimulus* Viá Boada & Villalta, 1966; *Tarracolimulus* Romero & Viá Boada, 1977; *Casterolimulus* Holland, Erickson & O'Brien, 1975; *Limulus* Müller, 1785; *Tachypleus* Leach, 1819 and *Carcinoscorpius* Pocock, 1902), which are all of post-Permian age, have a thoracetron like that of the moravurids. In addition, the only known moravurid carapace, that of *Xaniopyramis,* shows a continuous ophthalmic ridge sagittally, whereas the Limulidae diagnostically have no continuation of this ridge in front of the cardiac lobe (see Riek & Gill 1971).

The Carboniferous to Permian Paleolimulidae Raymond, 1944 (which may include, in addition to *Paleolimulus, Anacontium* Raymond, 1944; see Fisher 1982, fig. 1; Waterston 1985, p. 26) display an anteriorly continuous ophthalmic ridge and this feature has hitherto been known, with one or two exceptions, only from this family within the limuloids. *Rolfeia,* which was originally tentatively considered a paleolimulid but which will, in our forthcoming paper, be placed in a new monotypic family, shares this character, as does the Triassic *Limulitella* Størmer, 1952, according to the text-figures of Fisher (1981, fig. 3D) and Ponomarenko (1985, fig. 1), the latter genus having been considered a possible synonym of *Paleolimulus* by Riek & Gill (1971) and of uncertain family position by Waterston (1985). The paleolimulid thoracetron, though showing some similarity with that of the moravurids, including in *Paleolimulus avitus* itself probable homologues of the longitudinal pleural ridges and associated nodes (Dunbar 1923, pl. 2, p. 447), lacks the prominent *network* of ridges seen in the Moravuridae. Other younger limuloids, incidentally, seem also to have vestiges of the longitudinal pleural ridges, for example *Mesolimulus* (Størmer 1952, p. 637, fig. 1l; see also Fisher 1984, fig. 1c). Additionally, Dunbar (1923, p. 446) reported eight visible segments in the thoracetron of *P. avitus,* which is greater than the number apparent in the moravurids; however the count in *P. avitus* cannot be confirmed by examination of the photographs in Dunbar (1923) or Raymond (1944) and that in the moravurids is not entirely certain.

The enigmatic late Devonian Elleriidae Raymond, 1944, represented by just a single, incomplete thoracetron of *Elleria morani* (Eller, 1938b) from Pennsylvania, must also be mentioned. Like the Moravuridae, this family has very strong transverse pleural ridges, but it shows no evidence of longitudinal ones and also differs in the details of its axis. Fisher (1982, text-fig. 1) included *Elleria* Raymond, 1944 in the Bellinuroidea, without discussion, and it is difficult to follow this assignment in that the main characteristic of bellinuroids is the possession of free opisthosomal tergites, unless one assumes that the missing anterior portion of the *E. morani* thoracetron (see Raymond 1944, p. 497) showed free articulation. Bergström (1975) also put the Elleriidae in the Bellinuroidea, presumably on the same assumption, as his diagnosis of this superfamily included 'opisthosoma with articulated sclerites at least anteriorly'. It seems to us that the relationships and superfamily position of the Elleriidae remain uncertain.

The even more problematic Kiaeriidae Størmer, 1952, established on the basis of one very incomplete specimen of the only species, *Kiaeria limuloides* Størmer, 1934, which also shows strong pleural ribs, is in the present authors' opinion only questionably a xiphosurid.

Genus *Xaniopyramis* gen. nov.

Type Species. Xaniopyramis linseyi sp. nov.; Carboniferous, Namurian Series, Weardale, County Durham. By monotypy.

Derivation of name. Greek, *xanion,* a card for combing wool, and *pyramis,* an angular structure with a pointed apex, referring respectively to the fancied resemblance of the marginal opisthosomal spines and the tri- and quadriradiate ridged structures on the carapace and thoracetron.

Other species. None.

Diagnosis. A moravurid with a triradiate, ridged, pyramidal structure on the posterior part of the cheek, part of this structure forming the anterior boundary of the posteromarginal facet. Genal spine is narrow and three-fifths as long as carapace. Thoracetron with fourth axial ridge continued abaxially into a transverse pleural ridge and the longitudinal pleural ridge continued posteriorly beyond third transverse pleural ridge; it has (at least two, anteriorly positioned) curved spines radiating out from lateral margin and a small spine on pleural area sited just behind and abaxial to posterior

margin of axis; probable free lobe on anterolateral margin.

Discussion. There are numerous difficulties in comparing the Weardale specimen with the only known specimen of *Moravurus;* both are incomplete, most particularly the latter, and both suffer from preservational shortcomings, so it is difficult to assess to what extent some of the observed differences are real and of taxonomic importance. Nevertheless the Weardale specimen can be shown, even on present evidence, to be sufficiently distinct to merit establishing *Xaniopyramis* gen. nov. to accommodate it.

Xaniopyramis differs most obviously from *Moravurus* in possessing curved spines radiating from the thoracetron margin. It should be noted, however, that only a small proportion of this margin is known in *Moravurus,* and it is possible that spines remain undiscovered. If this is proved so, then this feature, used in combination, would become a familial rather than a generic character. The thoracetron outline in *Moravurus* was given (Přibyl 1967, p. 458, pl. 1, figs 1, 2) as smoothly subsemicircular; whereas that in *Xaniopyramis* is unknown for certain, our reconstruction leads us to believe that overall it was more subtriangular or subtrapezoidal in shape, and that in detail it possibly had a fluted edge also.

There is a definite difference in the pattern of pleural ridges between the two genera: *Moravurus* lacks the extension of the fourth axial ridge into a transverse pleural ridge and lacks any posterior continuation of the longitudinal ridge beyond the third transverse ridge, as is the case in *Xaniopyramis.* The small spine which is assumed to lie on the posterior termination of the longitudinal pleural ridge, and also the probable free lobe, both present in *Xaniopyramis,* are both apparently absent in *Moravurus.* The absence of the probable free lobe structure in *Moravurus,* given its presence in *Xaniopyramis,* is surprising and difficult to explain; the development of a free lobe marks a fundamental evolutionary change in xiphosurid morphology, a change that one expects to have been accomplished by all specimens placed in the same family. Perhaps this anomaly is preservational, any free lobe which *Moravurus* may have had having become detached from the main body of the thoracetron and lost.

Přibyl regarded *Moravurus* as having a short, blade-shaped telson with a median keel, this being formed by the sixth segment of the thoracetron. The telson of *Xaniopyramis* is unknown, and it seems likely that the so-called telson of *Moravurus* is simply the posterior part of the axis, a similar structure being present in the British genus (Fig. 5), and that the real telson of the Bohemian form is also missing.

The triradiate ridge on the carapace of *Xaniopyramis* (see species description) is unique to this genus within the xiphosurids. It could eventually be used to help characterize the Moravuridae, and not as at present *Xaniopyramis,* should *Moravurus* be found to possess it.

Occurrence: Known only from the lower Namurian of Weardale, County Durham.

Xaniopyramis linseyi sp. nov.
Figs 4-7A

Derivation of name. In recognition of the collector, T. K. Linsey.

Holotype. An incomplete carapace and thoracetron, HU P1986.1, Figs 4-7A.

Type stratum and locality. Upper Carboniferous, Namurian Series, probably from the Upper Limestone Group, from a horizon between the top of the Firestone Sill and beds just above the Upper Fell Top Limestone, (the upper part of the E_1 Zone, Pendleian Stage, to the lower part of the E_2 Zone, Arnsbergian Stage); stream section at a height of 540 m on the northern side of Noon Hill, 2.5 km SSW of Ireshopeburn village, Weardale, County Durham [NY 8526 3659] (Figs 1-3). A level from within the Pendleian part of this time interval is most likely (see section 1.2).

Additional material. None.

Diagnosis. As for the genus.

Description. Carapace is subsemicircular in outline, about twice as wide (tr.) at genal angle as long (sag.). Preophthalmic field moderately convex, slopes steeply downwards to a very shallow, narrow furrow that is continuous laterally and marks the inner limit of a very narrow carapace border which has a slender, slightly upturned rim. Cheek area slopes progressivly less steeply downward in an arc radiating from eye forward, then outward, then posteriorly toward genal angle. About midway between posterior part of ophthalmic ridge and lateral carapace margin, the cheek is sharply raised into a pyramidal structure comprising the triradiate junction of three ridges. The cheek ridge runs forward and slightly inward, fading out just posterior to a point transversely opposite the eye; a second, abaxial ridge runs outward and gently backwards toward genal angle; a third, adaxial ridge trends inward and backward, reaches presumed position of posterior margin of carapace outside ophthalmic ridge and is then continued as a longitudinal pleural ridge on opisthosoma. Posterior to adaxial and abaxial ridges and inside genal angle is a downward, backward facing posteromarginal facet. Genal spine is narrow and long, about three fifths the length of carapace, apparently does not continue backward curve of carapace margin but diverges outward from it (see section 3.2). Posterior margin of carapace not preserved.

Ophthalmic ridge anterior to eye is continuous, distinct and parabolic in outline; posteriorly its exact course is uncertain, seemingly gently curving more or less backward. Eyes positioned on highest part of carapace and about half-way between anterior and posterior margins; interocular distance about one-third the width of the carapace exclusive of genal spines. The cardiophthalmic region, at present seen depressed below the height of the ophthalmic ridge, presumably

lay originally at least on about the same level as or was raised somewhat above the height of this ridge (see section 3.1). Cardiac lobe appears to be tightly parabolic to wedge-shaped in outline, at posterior margin it is about one-quarter the width of the cardiophthalmic region, it is moderately raised above interophthalmic region which contains six lobate depressions, the anterior one being distinctly smaller than the rest. Sagittally, cardiac ridge projects posteriorly for a short distance from ophthalmic ridge.

Thoracetron overall outline unknown with certainty, but seemingly subtriangular to subtrapezoidal; maximum width about equal to or slightly less than that of carapace excluding genal spines. Probable free lobe (see section 3.2). Moderately convex (tr.) axis has five rings and a terminal piece, the two anterior ones with what appears to be a centrally positioned node. Axial furrows broad and shallow. Anteriorly the longitudinal pleural ridge runs backward and quite strongly inward, at its mid-length trends backward and only marginally inward, posteriorly turns more sharply inward again. Crossing the longitudinal pleural ridge there are at least four sharply raised transverse pleural ridges; the anterior one is convex forward and more or less directed transversely, the others are convex forward but curve progressively more backward in the posterior part of the thoracetron. Each axial ridge becomes somewhat more raised and broadens into a node-like structure sagitally; abaxially where each transverse pleural ridge crosses a longitudinal pleural ridge a raised quadriradiate node is formed. Pleurae become narrower (exs.) posteriorly; each rib expands in width (exs.) laterally from axis. Between axial furrow and longitudinal pleural ridge, exclusive of raised transverse pleural ridges, thoracetron is more or less flat; abaxial to longitudinal pleural ridge it falls moderately steeply towards margin, but must flatten out and become more horizontal near to margin, as indicated by sediment cover on this part and also by the level of the horizontal plane on which the opisthosomal spines lie. At least the two more anterior transverse pleural ridges are each produced laterally into an opisthosomal spine; at least one spine is slightly swollen at its base where it contacts the thoracetron margin; each spine curves gently posteriorly. Very small spine present posteriorly which appears to lie on projected line of longitudinal ridge. Sediment masks nearly all posterior part of thoracetron, but behind last completely visible axial ring it is generally depressed except for a slightly raised, roughly diamond-shaped area with a gentle median ridge which is presumed to represent the terminal axial piece.

Discussion. See that for the genus.

5. FUNCTIONAL MORPHOLOGY

5.1. The pleural ridges

One of the most characteristic features of *Xaniopyramis* is its highly ridged thoracetron. The transverse pleural ridges are considered to represent ancestral tergite boundaries, whereas the longitudinal pleural ridges are an innovation which persists in the Limuloidea. The functional advantages of opisthosomal fusion, independently acquired by limuloids and euproopoids, were enumerated by Fisher (1981, p.53). Opisthosomal fusion was accompanied by increased degrees of articulation of both the prosoma—opisthosoma joint and the telson and also greater telson length in order to achieve the body flexibility necessary for righting the overturned animal and for burrowing (Fisher 1981, 1982). It is for this reason that *Xaniopyramis* is reconstructed with a long telson (Fig. 7). However, a rigid thoracetron would be susceptible to bending stress in the sagittal direction during these activities and longitudinal ridges and furrows would strengthen it against this (J. E. Dalingwater, oral comm. 1985).

The only comparable limulicines with pronounced transverse pleural ridges are *Moravurus* and *Elleria,* about which little is known, and the euproopoids. Fisher (1979) considered the transverse pleural ridges of *Euproops rotundatus* (Prestwich, 1840) to have aided mimicry of the anthracomartid arachnid *Maiocercus carbonis* (Howard & Thomas, 1896) with which it commonly occurs. No obvious potential mimic exists for *Xaniopyramis,* and the existence of the phenomenon seems unlikely for a large animal capable of self-defence in other ways. Indeed, the pattern of the thoracetron of *Xaniopyramis* is striking and even when partially buried it would have been conspicuous; thus any suggestion of cryptic patterning can also be ruled out, though its function as a warning or recognition device is possible. The function of the transverse pleural ridges in distributing sediments during burial in euproopoids (Fisher 1979) cannot apply to *Xaniopyramis* since the longitudinal pleural ridges would have interfered with this effect. Structurally, transverse ridges would have strengthened the thoracetron, and may have been useful during ecdysis. The function of the thoracetron pattern thus remains poorly understood.

5.2. Enrollment

Bergström (1975) and Fisher (1977a, b, 1981) discussed enrollment in Palaeozoic xiphosurans and their work has recently been summarized by Waterston (1985). Bergström (1975) distinguished between true (sphaeroidal) enrollment, necessitating the presence of at least one free tergite in the opisthosoma (this capability is thus restricted to the Bellinuroidea within the Limulicina), and coaptation ('folding up' *sensu* Bergström 1975) in which the animal flexes at the prosoma—opisthosoma articulation and the prosomal and opisthosomal doublures are adpressed. The latter mechanism occurs in euproopoids (Bergström 1975; Fisher 1977b) but not in limuloids, except possibly in some paleolimulids (see below). Limuloids, with their more streamlined, trapezoidal thoracetron, adopted burial rather than enrollment as their primary defence mechanism (Waterston 1985). Fisher (1981) pointed out that the morphology of the occlusive regions, the

prosomal and opisthosomal doublures, is of prime importance, rather than the general outline of the thoracetron. Nevertheless, the sizes and shapes of carapace and thoracetron in a coapting animal cannot differ markedly. It is fortunate that the edges of the doublures are readily identifiable in many fossil xiphosurans. Waterston (1985) considered *Rolfeia* to have been capable of coaptation but to have preferred burial as its main defence strategy; judging from his reconstruction (Waterston 1985, fig. 3), *Rolfeia* was not well adapted for coaptation since the thoracetron is considerably longer and narrower than the prosoma and the doublures do not match in shape, so complete occlusion of the ventral surface would not have been possible. In *Paleolimulus longispinus* Schram, 1979, from the Namurian Bear Gulch Limestone of Montana, the semicircular inner margin of the opisthosomal doublure appears to match exactly that of the prosomal doublure (Schram 1979, fig. 1, although his reconstruction, fig. 2, does not show this), so it may be concluded that coaptation was a useful means of defence in this species.

The reconstruction of *Xaniopyramis* (Fig. 7) shows the thoracetron to be considerably smaller than the carapace, and of a roughly trapezoidal shape, whereas the carapace is subsemicircular. Thus it appears that coaptation was probably an inefficient means of defence for this animal, but there is evidence favouring burial as a protective strategy as outlined below.

5.3. Burrowing and swimming

Several authors have described burrowing in modern *Limulus,* including Eldredge (1970), Vosatka (1970) and Fisher (1975), and a summary of the implications for functional morphological investigations of fossil limuloids was given by Waterston (1985). The method of burial requires a highly vaulted carapace to allow room for leverage of propulsive appendages, and dorso-ventrally flattened limuloids were less adapted for burrowing as a consequence (Fisher 1975). When buried, there is the problem of ensuring an adequate stream of water to irrigate the gills yet preventing them getting clogged with sediment. To this end, *Limulus* draws water under the opisthosoma through the channel between the carapace and thoracetron (Eldredge 1970). To minimize the amount of sediment entering the channel, it is guarded by long bristles and roofed by the free lobe; Fisher (1981) pointed out that the presence of a free lobe in limuloids is an indication of their burrowing habit. *Xaniopyramis* exhibits morphological features consistent with a burrowing habit: a vaulted carapace and probably a free lobe; additionally, preservation of the specimen in a shallow marine sandstone suggests that the animal lived in an environment conducive to a burrowing habit (see section 6).

In addition to the vaulted carapace and free lobes which are characteristic of benthic forms, and not of swimmers that lack these (Fisher 1975), the heavily sculptured thoracetron and long genal spines of *Xaniopyramis* are uncharacteristic of limuloids which habitually swim. Long spines are no hindrance to small swimming xiphosurids like *Euroops danae* (Meek & Worthen, 1865) (Fisher 1977b) and *Rolfeia* (Waterston 1985) and can be advantageous in aiding passive settling of the coapted animal as a defence mechanism, but larger swimming animals lack spines which minimizes drag effects. Such forms, for example *Dubbolimulus* Pickett, 1984, have the sculpture of carapace and thoracetron effaced thereby reducing drag, whereas *Xaniopyramis* clearly does not. Long, movable opisthosomal spines could be considered a hindrance to swimming which may be why they are absent in *Dubbolimulus* (Pickett 1984). However, even limuloids which habitually swim need to settle on the substrate, when the mechanoreceptive function of the spines in monitoring the position of opisthosoma relative to the substrate would be useful (Fisher 1981). Thus forms well adapted for swimming, like *Mesolimulus* (Fisher 1975), bear movable opisthosomal spines and this character is of little use in deducing mode of life. The suggestion of Waterston (1985) that the length and attitude of these movable spines may be related to substrate type could repay further investigation.

6. PALAEOECOLOGY

6.1. The sediment

The matrix surrounding the fossil is composed of quartz (about 55%), mica (about 15% with biotite more abundant than muscovite), feldspar (about 15%), subsidiary opaque minerals and traces of hornblende. The micas and feldspars are commonly altered to clay minerals. The cementation is of quartz overgrowths with clays filling some pore spaces. The rock may be termed a micaceous, submature arenite, with predominantly fine, moderately well sorted grains which appear subrounded.

6.2. Taphonomy

There are no sedimentary structures visible on the block containing the specimen which could indicate with certainty its way-up. It has been assumed that the xiphosurid was at rest on the sediment surface convex upwards in a hydrodynamically stable position. In front and to the right of the specimen there is a slightly skewed, crescentic, sharply edged (particularly anteriorly) break in the sediment surface, running subparallel to the prosomal margin. The latter lies below the height of the sediment platform (bedding plane) outside this crescent, and between it and the crescent the sediment surface is strongly concave upwards (Figs 4-6).

If the animal had been in the process of shallow burrowing, and retracted slightly, this might have produced a collapse of sediment around the prosoma to give the present configuration. However, observations of burrowing in *Limulus* have shown that it is normal for a convex-upward rise of sediment to be formed around

the prosoma, and that subsequent reworking of the sediment often removes this raised rim to leave only the main subcircular depression that has been excavated by the prosomal appendages (Eldredge 1970; Halsey *et al.* 1973; Miller 1982).

A second explanation for the crescentic structure is that it was formed by unidirectional current scour. To test this hypothesis a *Limulus* specimen was placed in a flume tank on a bed of loose, fine to medium grained sand, and facing into the current flow. A crescentic, concave excavation was produced which was closely comparable with that of the fossil example. Additionally, in the fossil it is noticeable that the right cusp of the crescent is appreciably longer than the left. By orienting the *Limulus* oblique to the prevailing current in the flume, a close replica in terms of depth, shape and orientation of the concave structure in front of the fossil example was obtained (Fig. 8). The similarity of the recent and fossil examples leaves little doubt that the crescentic structure represents a current scour-mark formed when the animal was obliquely facing a water flow from the right anterior side. Subsequent rapid deposition of sand must have occurred in order to preserve the sharp-edged nature of the scour-mark margin.

Fig. 8. Recent *Limulus* in flume tank on a bed of fine sand after a current of water passed over it. Dorsal view, × 0.8. Arrow indicates direction of current. Note the current scour in front and to the right of the specimen and compare with Fig. 4.

6.3. The nature of the xiphosurid fossil

If the first, less likely, burrowing explanation of the crescentic structure were correct (see section 6.2), then the fossil must represent the remains of the animal itself rather than a moult. Either a living animal or a moult might give rise to a current scour, though probably a much lighter moult would have been swept away by such a current and not have offered the stability and resistance necessary for a scour-mark to have formed. It seems probable, then, that we are dealing with the remains of the actual animal, which may have been newly moulted since there is some evidence to suggest that the cuticle was soft and pliant (see section 3.1).

6.4 The nature of the environment

During the early Namurian, the Alston Block was subjected to what Ramsbottom (1974, pp. 84-86) termed a modified Yoredale facies type of sedimentation, distinct from the standard Yoredale sedimentation of the upper Dinantian. This modified Yoredale facies is essentially a thin, shallow-water sequence found in northern England, typically on the Alston and Askrigg blocks, and is coeval with the much thicker Millstone Grit of the Central Province basin to the south (Ramsbottom 1969, p.230, figs 18, 19). The Millstone Grit clastics were derived from more northerly or north-easterly positioned deltas, but deltaic conditions also prevailed at certain times on the blocks. Elliot (1975) has described the progradation and abandonment of a delta lobe in the earliest Namurian times, during the Great Limestone to Little Limestone interval, which covered the Alston Block from Weardale in the north to Stainmore in the south.

Recent xiphosurids inhabit a wide variety of subenvironments close to the coastline, from shallow-water, fully marine to brackish estuarine situations (and probably even freshwater situations; see Sekiguchi & Nakamura 1979, p.40); individually they are tolerant of wide variations in salinity and temperature (Fisher 1984, p.203). Fossil xiphosurids are thought to have inhabited a similar environmental spectrum (shallow marine to fresh water), and it has been claimed (Fisher 1979) that *Euproops* from the Westphalian was amphibious and engaged in subaerial activity. What environment, then, did *Xaniopyramis* inhabit, given this environmental tolerance of xiphosurids and the continually changing conditions associated with the shallow marine to deltaic early Namurian sediments of the Alston Block? In the absence of other fossils in the sandstone block containing *Xaniopyramis* the answer to this question must be sought in the sediments and facies relationships.

There is, even on sedimentological criteria, no clear answer. The specimen was not found *in situ,* and the nature of the sediment surface on which the *Xaniopyramis* specimen was resting is unknown since

the external mould is preserved in sandstone which would have been deposited on top of the surface supporting the animal. The submature nature of the sandstone, with mica and feldspars (see section 6.1) suggests that reworking of the sediment was not severe. Dr C. J. Percival, who has recently completed a doctoral thesis (University of Durham, 1981) on the quartz arenites and ganisters of the northern Pennines, has kindly examined the *Xaniopyramis* sandstone block in thin section and hand specimen. He commented as follows: "I would think that the sandstone is a deltaic sandstone which has undergone a limited amount of reworking during a marine transgression (and hence the specimen is marine). I would think that it is most likely to come from the base of one of the Rookhope Shell beds . . . but I am slightly surprised at the lack of any carbonate in the sandstone. This may mean that it comes from just below the shell bed, and represents the initial transgressive phase prior to the establishment of prime shell-bed conditions (main transgressive phase, negligible sediment input)".

It seems that the *Xaniopyramis* specimen lived in a shallow marine sea which was possibly transgressive, though it is still possible that it was actually resting on a surface of more near-shore deltaic facies. *Moravurus* came from the lower Namurian Štúr marine band, which displays a faunal association, typical for this marine horizon, of *Lingula mytiloides, Anthraconeilo oblongum, A. laevirostrum, Polidevcia vasiceki, P. sharmani and Sanguinolites interruptus* (Přibyl 1967, p.459). However, it is unclear from Přibyl whether this fauna is actually on the same bedding plane of the core which yielded *Moravurus,* or merely in the same lithological units as the *Moravurus* specimen.

6.5. Trace fossil evidence of xiphosurids from the British Namurian

The only other evidence of xiphosurids from the British Namurian is that of trace fossils. Hardy (1970) described resting traces from the Yeadonian Upper Haslingden Flags of Lancashire, which Chisholm (1983) assigned to *Limulicubichnus rossendalensis* (Hardy, 1970). Chisholm (1983) discussed some walking and part-swimming trackways and trails, referred to *Kouphichnium* aff. *variabilis* (Linck, 1949), from the same horizon and locality. Chisholm later (1986) described xiphosurid burrows as *Aulichnites? bradfordensis* Chisholm, 1986 from sandy siltstones above the Kinderscoutian Butterly Marine Band of Standedge, West Yorkshire, and a similar example has recently been found at the same horizon in Derbyshire (Dr R. M. C. Eagar, oral comm. 1986).

L. rossendalensis and *K.* aff. *variabilis* are believed to have been made by the same xiphosurid species (Chisholm 1986, p. 624). Either *Bellinurus* or *Euproops* (each of which has been recorded from the Westphalian of Lancashire, Baldwin 1902, 1903, 1905) is thought to have produced all the above traces; both Hardy (1970, p. 189) and Chisholm (1983, p. 144; 1986, p. 622) claimed *Bellinurus* as the likeliest candidate. The maximum widths recorded for *L. rossendalensis, K.* aff. *variabilis* and *A.? bradfordensis* were approximately 17mm, 30mm, and 25mm respectively (Hardy 1970, p. 189; Chisholm 1983, p. 40, 1986, p. 620) but, disregarding the greater size of *Xaniopyramis,* the traces show no morphological features which would preclude their formation by this animal.

The Upper Haslingden Flags were believed to represent mouth-bar deposits of a delta (Chisholm 1983; Collinson & Banks 1975), and similarly the Standedge sediments were thought to have been deposited in a river mouth or interdistributary bay environment (Chisholm 1986). A reassessment of the xiphosurid ichnofauna of the Upper Haslingden Flags by Eagar *et al.* (1985, pp. 129–131, 139) concluded that it indicates a non-marine, shallow-water situation which was subject to periodic, climate-induced fluctuations in water level causing specimens to become stranded on mudflats. This supports the non-marine environmental interpretation of Hardy (1970, p. 189) for the Haslingden traces, and Chisholm (1983, pp. 39, 44) suggested that whilst the mouth-bar was being submerged under a stretch of open water, it was at times subaerially exposed. Thus there is considerable similarity between the environments suggested above for *Xaniopyramis* and those indicated for the xiphosurid ichnofaunas.

7. PALAEOGEOGRAPHY

Ramsbottom (1971, fig. 1) depicted Great Britain, except for south-west England, as lying in middle Namurian times a few degrees north of the equator, at the western end of a narrow, generally north-east to south-west trending seaway. The seaway ran parallel to the northern margin of Tethys, from which it was separated by the linear Variscan landmass stretching from western France to the Black Sea area. The northern shoreline of this seaway ran from the north of Scotland to Byelorussia to the east, and formed the eastern part of the North Atlantic continent, which included the Baltic region, Scandinavia and much of North America. Ziegler (1982, map 10) provided a detailed palaeogeographic map of N.W. Europe during Namurian times, showing this narrow seaway sandwiched between North Atlantic and Variscan continents. Ramsbottom (1971, p. 1398) also noted that during the early Namurian there was interchange of goniatite faunas between Russia and western Europe via Poland, a biogeographic connection already claimed for certain bethnic elements, for example brachiopods, in Scottish rocks of this age (Wilson 1967). Ramsbottom further suggested (1971, p. 1395; 1974, p. 87), on the basis of wind distribution patterns, that the prevailing marine current direction in the seaway would have been towards the west, from central and eastern Europe, and that this was the dominant direction of faunal interchange at this time, rather than from west to east.

The confamilial relationship of *Xaniopyramis* from northern England and *Moravurus* from Bohemia upholds the idea of a lower Namurian faunal link between central and western Europe.

Limulus is confined throughout its life to shallow, nearshore marine areas; the juveniles in particular, which develop from eggs placed high in the intertidal zone, stay all the year on intertidal mudflats. Adults typically occur in slightly more offshore, sandier environments, though normally still within depths of less than 50m (Fisher 1984, p.202; Rudloe 1979, p.27; Shuster 1979, p.15). In addition, fossil xiphosurids are not, to our knowledge, known from deep water offshore marine facies, so on present evidence it seems more probable that their spread would have been determined by the longshore movement of adults, rather than by the oceanic dispersal of juveniles or adults, as in brachiopods and goniatites.

Moravia was situated on the southern, Variscan shore of the Namurian European seaway whereas the Alston Block was closer to and more geologically associated with the northern, North Atlantic landmass (see Ramsbottom 1969, p. 231). The most obvious moravurid migration route would have been via the Wales-Brabant massif, which connects central England to Belgium and approaches very close to the Variscan continent (Ziegler 1982, map 10). Another possible routeway linking the northern and southern shorelines would have been a connection between the Byelorussian high to the north and Poland to the south. The Namurian seaway was at its narrowest at this point, and as drawn by Ziegler it was here less than 200km wide. It was in this area that the open sea connection between Russia and western Europe was severed in late Namurian (G) times, and with it the flow of goniatite faunas (Ramsbottom 1971, p.1398). Perhaps even in early Namurian times this stretch of water was sufficiently shallow, or dotted with islands, to facilitate xiphosurid migration between the Variscan and North Atlantic shores.

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