SOFT-SEDIMENT ADAPTATIONS IN A NEW SILURIAN GASTROPOD FROM CENTRAL ASIA

by A. P. GUBANOV, J. S. PEEL *and* I. A. PIANOVSKAYA

ABSTRACT. Specimens of the gastropod *Isfarispira septata* gen. et sp. nov., from the Silurian of Central Asia, are characterized by a large, lenticular, multi-whorled shell with a flattened base, a low rate of expansion of the broad whorls, internal septa at intermediate growth stages and a prominent circumbilical flange which closed off much of the umbilicus. These morphological features reflect adaptation to life on a soft substratum, collectively serving to inhibit sinking into the soft sediment by increasing the area of the basal surface. *I. septata* is interpreted as a sedentary, or only infrequently mobile gastropod.

THE presence of an internal plug (or septum) closing off the earliest stages of the shell is not an unusual phenomenon in Palaeozoic gastropod molluscs (Yochelson 1971). Indeed, this morphological feature is not restricted to gastropods, being also documented in the Class Helcionelloida (Rasetti 1957; see Peel 1991*a*) and the Class Tergomya (Yochelson *et al.* 1973; Webers *et al.* 1992). Several non-molluscan, Cambrian, tube-like fossils, such as *Camarotheca* and *Actinotheca* (Fischer 1962; Bengtson *et al.* 1990), also developed internal septation.

An internal apical plug or septum in the earliest growth stages of gastropods is usually detectable as a rounded termination of the internal mould, although septa and calcite spar filling the closed-off portion also may be visible in cross sections (see Lindström 1884, pl. 13, figs 30, 36; pl. 15, fig. 5). In contrast to the septa of cephalopods, gastropod septa are not penetrated by a siphuncle or other structure and areas of the shell cavity located adapically of each septum are thus sealed off from the body cavity by the septum itself.

The presence of repeated septa at later growth stages is relatively rare in Palaeozoic gastropods and only a few examples have been documented. Notable amongst these are two Devonian gastropods described by Yochelson (1966, 1971). *Nevadaspira* is an open coiled form in which Yochelson (1971) described abundant closely spaced septa in the early and penultimate whorls. Similar septa are known in a variety of other, often loosely coiled, euomphalacean gastropods, although they are not usually as numerous as in *Nevadaspira* (Yochelson 1971). *Arctomphalus* has a more tightly coiled, low spired shell form, but Yochelson (1966, 1971) recorded at least ten septa spaced at intervals averaging 2·5 mm. Linsley (1978*a*) considered *Arctomphalus grandis* to be the male(?) sexual dimorph of *Omphalocirrus goldfussi*; he also described abundant septa in the related omphalocirrid *Hypomphalocirrus*. Illustrations of the rare, open coiled gastropod *Phanerotinus*, from the Carboniferous of the United Kingdom, presented by Morris and Cleevely (1981) indicate the occurrence of septa to within about one whorl of the preserved aperture, with three or four earlier whorls sealed off from the body chamber. The Ordovician to Silurian *Lytospira* also has an open coiled shell with abundant septa in the early whorls (Koken and Perner 1925).

Cook (1993) described abundant internal septa in *Fletcherviewia septata* from the Devonian of Australia. The record is of particular interest in that septation is developed in a tightly coiled, high spired gastropod, in contrast to occurrences of multiple septation in the low spired *Nevadispira*, *Phanerotinus*, *Lytospira*, *Arctomphalus* (= *Omphalocirrus*) and *Hypomphalocirrus*.

Here we describe septation in a large, lenticular gastropod from the Silurian of Central Asia, proposed as *Isfarispira septata* gen. et sp. nov. Together with other features of the shell, such as the broad whorl cross-section, low spire, low rate of whorl expansion, and development of a prominent circumbilical flange, the development of internal septation in *Isfarispira* results from adaptation to life in a soft sediment environment. In general, however, there is no reason to assume any direct correlation between the occurrence of septation in fossil gastropods and soft sediment environments.

[Palaeontology, Vol. 38, Part 4, 1995, pp. 831–842, 1 pl.]

While septation indicates withdrawal of the gastropod animal from the early portion of its shell, published descriptions suggest that this withdrawal was a response to several different circumstances.

GEOLOGICAL SETTING

Specimens described here as *Isfarispira septata* gen. et sp. nov. were collected from the Chorkuin Formation in the Pschemack Mountains of Central Asia which form part of the western segment of Southern Tien Shan (Text-fig. 1). The succession in this area is tectonically deformed into a series of nappes, but includes sedimentary rocks of Middle and Upper Cambrian, Silurian, Devonian and Carboniferous ages. The Chorkuin Formation is of Silurian age, straddling the Llandovery-Wenlock boundary. It is composed mainly of siltstones, but the gastropods are preserved in limestone lenses. All fossils were collected by Irina A. Pianovskaya who also described the section. Associated fossils include the cephalopods *Geisonoceras kureikense* and *Edenoceras hiliferum* (determined by E. I. Miagkova), the graptolite *Monograptus* sp. (?ex group *M. priodon*, determined by G. W. Pianovsky) and the trilobites *Encrinurus punctatus* and *Otarion* sp. (determined by T. I. Hajrullina).

SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797
Class GASTROPODA Cuvier, 1797
Subclass PROSOBRANCHIA Milne Edwards, 1848
Order ARCHAEOGASTROPODA Thiele, 1925
Superfamily EUOMPHALACEA Koninck, 1881
Family OMPHALOTROCHIDAE Knight, 1945?

Genus ISFARISPIRA gen. nov.

Derivation of name. From the Isfara river, which lies to the east of the type locality in the Pschemack Mountains (Text-fig. 1).

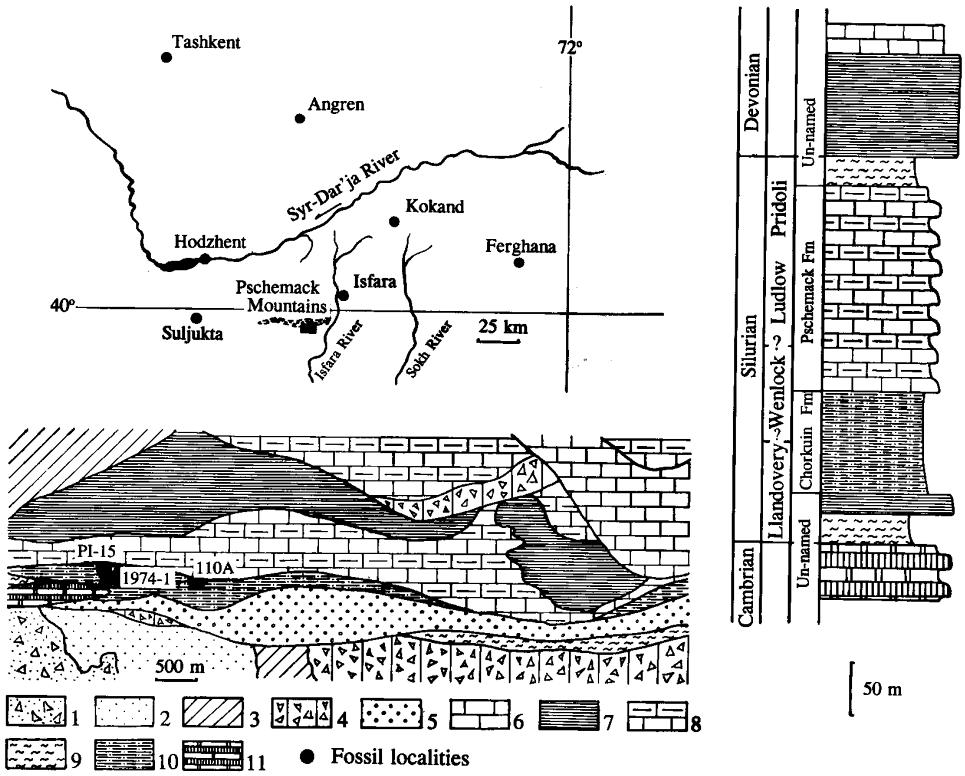
Type species. *Isfarispira septata* gen. et sp. nov., from the Chorkuin Formation, Silurian, Central Asia (Text-fig. 1).

Diagnosis. Large, lenticular gastropod with more than ten slowly expanding whorls and a radial aperture. Umbilicus largely closed by a blade-like circumbilical flange, extending adumbilically as a continuation of the shallowly convex base. Shell interior with numerous adaperturally concave septa.

Remarks. In terms of its lenticular form, *Isfarispira* is morphologically reminiscent of *Liospira* which is widely distributed in Middle Ordovician and Silurian strata (Ulrich and Scofield 1897; Knight *et al*. 1960; Peel 1977). *Isfarispira* is readily distinguished from this genus, however, by its much greater size (more than 80 mm in diameter compared with the 20–30 mm of *Liospira*), greater number of more slowly expanding whorls and absence of the deep peripheral sinus and slit, and resultant selenizone. As in *Isfarispira*, the umbilicus in *Liospira* is often partially or completely closed.

The low rate of whorl expansion invites comparison of *Isfarispira* with Early Ordovician genera such as *Ophileta* and *Ozarkispira*, in particular when the genera are compared in apical view (cf. Knight 1941; Knight *et al*. 1960). *Isfarispira* has a narrower umbilicus, however, with whorls at least twice as wide as high, and the umbilicus is closed by the prominent circumbilical flange; the umbilicus is widely phaneromphalous in the Early Ordovician genera.

Grantlandispira, from the Silurian of North Greenland (Peel 1984*a*), differs from *Isfarispira* in having a higher spired and pronounced cyrtoconoid form, although both genera have many whorls. In *Grantlandispira* the umbilicus is almost closed by a massive circumbilical flange, much more robust than the thin circumbilical plate of *Isfarispira*. In addition, ornamentation on the upper



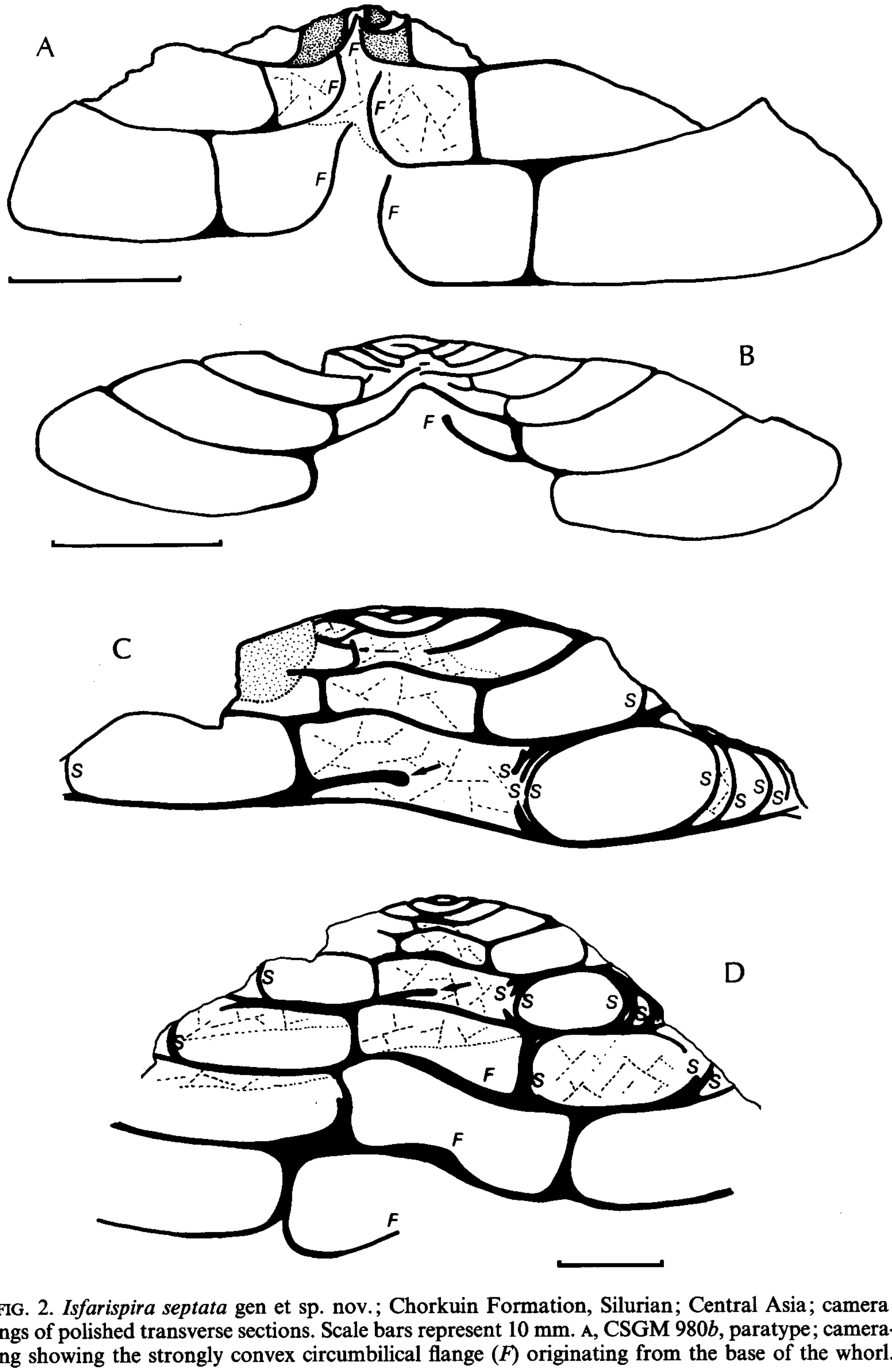
TEXT-FIG. 1. Derivation of *Isfarispira septata* gen. et sp. nov. from the Chorkuin Formation of the Pschemack Mountains, Central Asia; localities are discussed in the text. Lithologies: 1, alluvial deposits; 2, sandstones and gritstones; 3, clays; 4, olistostromes; 5, conglomerates; 6, dolomitic limestones; 7, black cherts; 8, alternations of limestones, clayey limestones and shales; 9; clay shales; 10, siltstones; 11, alternations of cherty rocks and dolomites.

whorl surface of the Greenland genus indicates a sub-sutural sinus which is seemingly not present in *Isfarispira*. Some species of the Devonian *Orecopia* may also have lenticular shells with a relatively high number of whorls (Pedder 1966) but these can be distinguished from *Isfarispira* by the narrower umbilicus, sub-circular whorl profile and the sub-sutural sinus.

Planitrochus, from the Upper Silurian of Bohemia, has a lenticular form, but with fewer whorls than *Isfarispira*; it also is distinguished by its sub-tangential aperture, and the lack of the prominent circumbilical flange (Knight 1941). *Kiaeromphalus*, from the Lower Silurian of Norway (Peel and Yochelson 1976), resembles *Isfarispira* in size and general form. It is distinguished by its more convex whorls with a rounded periphery, and by the open umbilicus.

Isfarispira is morphologically quite distinct from other described multi-septate gastropods, such as the open coiled *Nevadaspira*, *Lytospira* and *Phanerotinus* (Koken and Perner 1925; Yochelson 1971; Morris and Cleevely 1981), the low spired *Omphalocirrus* and *Hypomphalocirrus* (Linsley 1978*a*) and the high spired *Fletcherviewia* (Cook 1993).

In the classification of gastropods employed by Knight *et al.* (1960), *Isfarispira* is tentatively assigned to the Omphalotrochidae.



TEXT-FIG. 2. *Isfarispira septata* gen et sp. nov.; Chorkuin Formation, Silurian; Central Asia; camera lucida drawings of polished transverse sections. Scale bars represent 10 mm. A, CSGM 980*b*, paratype; camera-lucida drawing showing the strongly convex circumbilical flange (*F*) originating from the base of the whorl. Early

Isfarispira septata gen. et sp. nov.

Plate 1; Text-figure 2

Ophileta? aff. *perlata* (Hall, 1852); Mironova 1993, p. 7, pl. 1, fig. 1a–b
Pycnotrochus viator Perner, 1907; Mironova 1993, p. 6, pl. 1, fig. 3a–b

Derivation of name. With reference to the abundant internal septa.

Holotype. Palaeontological Collections of the Central Siberian Geological Museum (CSGM), Novosibirsk, Russia, 980*a*; Silurian; Chorkuin Formation, locality PI-15, Central Asia (Text-fig. 1).

Paratypes. CSGM 980*b*, from the same collection as the holotype; CSGM 980*c*, from locality 110A; CSGM 980*d–f*, from locality 1974-1. Silurian; Chorkuin Formation.

Description. At least ten whorls are present. The large lenticular shell is divided into upper and lower surfaces by the prominent peripheral angulation; the shell height varies from three-eighths to about half of the diameter. Sutural indentation is very slight. The sides of the low spire vary from slightly convex, such that the shell is weakly cyrtoconoid, to almost flat, but become shallowly concave in the latest growth stage because of an increase in the shell width at the transition to the final whorl. Early growth stages are poorly known. The width of the whorl in cross section, measured perpendicular to the axis of coiling, is about twice the height. The lower (basal) and upper (parietal) walls become increasingly parallel with growth of the shell, such that the two surfaces are both perpendicular to the axis of coiling in the umbilical region in the latest growth stage, but curve slightly adapically as the angular periphery is approached; the base is shallowly convex. The outer whorl surface is very shallowly convex between the periphery and the suture with the previous whorl, more so in early whorls. The final whorl is more noticeably flattened. The umbilical wall is sub-parallel to the axis of coiling and passes angularly into the lower and upper whorl surfaces.

The aperture is radial. Poorly preserved growth lines on the base of the holotype are shallowly convex adaperturally. In the same specimen, very poorly preserved growth lines on the outer whorl surface near the aperture are very slightly concave (adaperturally) as they traverse the outer whorl surface, with adapical obliquity, towards the periphery. Thus, there is a very shallow peripheral sinus, but there is no evidence to suggest the presence of a slit and selenizone. The umbilicus is seen to be wide in cross section but it is closed by a blade-like circumbilical flange which extends from the umbilical shoulder, as a continuation of the base, into the umbilicus. In some specimens, this flange extends across the umbilicus towards the umbilical suture a half whorl previously. In other specimens, the flange curves with increasing convexity towards the axial region. The flange is apparently narrower in the immediate vicinity of the aperture, with a thickened termination, but seems to attain its full extent within a whorl back from the apertural margin.

The shell interior is traversed by abundant septa which are concave adaperturally. In the holotype the body chamber seems to extend over at least one and three-quarter whorls. Adapical of this point, a number of septa are visible but they appear to be irregularly spaced. In cross section, septa are usually visible near the whorl periphery as adaxially concave surfaces which are less angular than the adjacent whorl periphery. The coalescence of septa in the area of the periphery and suture produces a thickening of the shell which gives some internal moulds a slightly gradate profile. The shell itself is seemingly quite thin, relative to the large size of the gastropod, but the flange and umbilical wall appear to be thickened at the aperture in the holotype.

Remarks. The small amount of material available illustrates quite considerable variation in the height of the spire. The holotype is relatively low spired, with height being about three-eighths of the maximum preserved diameter. Two paratypes are noticeably more high spired, with a more gradate profile, although the step-like profile has been emphasized by weathering; there are

whorls are filled with dark calcite spar (stippled); at intermediate growth stages, white calcite spar fills the umbilicus and the tube-like space between the upper surface of the flange and the base of the previous whorl. B, CSGM 980*d*, paratype; note the development of the circumbilical flange (*F*) about one whorl back from the preserved final growth stage. C–D, CSGM 980*c*, paratype; showing multiple septa (*S*) and the circumbilical flange (*F*) appearing to cross the umbilicus in the excentric section. Arrows locate the same flange in the enlargement (s) of the apical area. Note the white calcite spar in the umbilicus and as geopetal fills in intermediate whorls; the recrystallized area (stippled) in C is not related to the fossil.

insufficient grounds to suggest that these more gradate forms should be assigned to another species. The specimens, as a whole, are indifferently preserved, particularly with regard to details of the shell exterior.

Mironova (1993) assigned specimens from the same horizon and locality as the holotype of *Isfarispira septata* to *Ophileta*? aff. *perlata* and *Pycnotrochus viator*. Her illustrations show respectively low and higher spired specimens which fall within the range of variation of the current sample. Thus, we have no hesitation in placing Mironova's specimens within *Isfarispira septata*. Her illustration of the base (Mironova 1993, pl. 1, fig. 3b) clearly shows the shallowly convex growth lines and the circumbilical flange.

The relationship of *Isfarispira septata* to *Pleurotomaria perlata* is uncertain. Hall (1852) described the latter species on the basis of imperfect internal moulds from the Lower Silurian of Galt, Ontario, Canada. The scant references to other early reports from North America were summarized by Bassler (1915, p. 747). Hall (1852, pl. 84, fig. 5a–c) clearly illustrated the lenticular form, with numerous slowly expanding whorls, typical of *Isfarispira*, but the nature of the umbilicus, the form of the aperture, and the presence or absence of septa are not known.

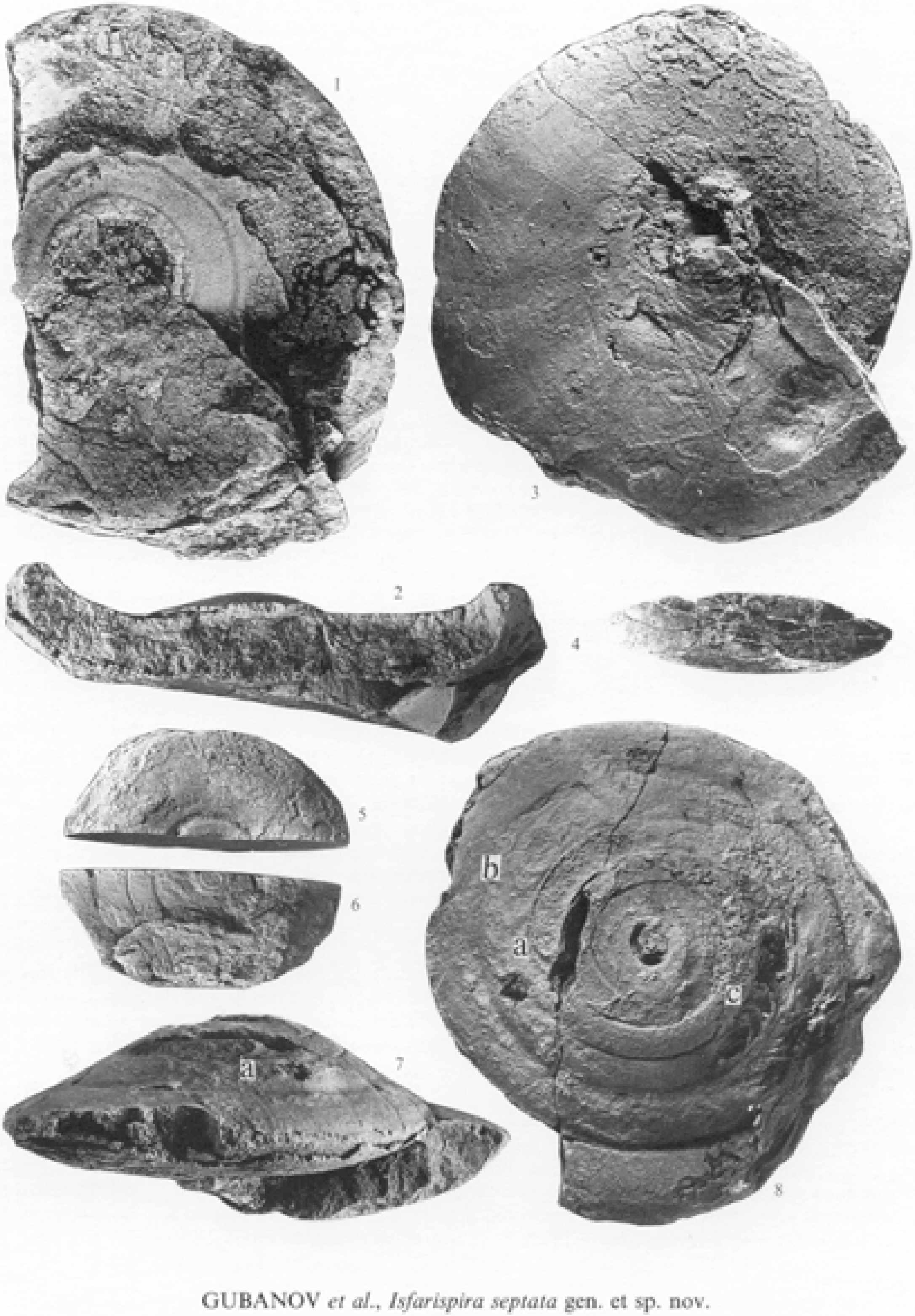
Williams (1919, pl. 24, fig. 1a–b) reproduced good photographs of an internal mould also from Galt, Ontario, in apical and umbilical views, but gave no description. The specimen has a maximum preserved diameter of almost 100 mm, measured from the illustration. In umbilical views (Williams 1919, pl. 24, fig. 1b) the internal mould clearly demonstrates the perpendicular relationship of the lower (basal) whorl surface to the umbilical wall, producing a step-like umbilical profile, seen also in *Isfarispira septata*. There is no indication, however, of the presence of a circumbilical flange. Whiteaves (1884, p. 75) did not illustrate Hall's (1852) species, which he knew only from internal moulds from localities at Galt, Hespeler, Elora and Belwood, but commented upon its large size, compressed lenticular form, acutely angular periphery and deep, but rather narrow umbilicus. He did not question its systematic placement with other pleurotomarians, which implies that he believed a peripheral slit and selenizone to be present, although he made no record of such features. Whiteaves (1906, p. 332) quoted from an extract from a letter from E. O. Ulrich suggesting that the species should be referred to *Liospira* which has a well developed peripheral slit and selenizone. In following this practice, Whiteaves reiterated that only poor internal moulds were available to him.

Dolomite internal moulds from localities in the Chicago to Milwaukee region in the collections of the National Museum of Natural History, Washington DC, demonstrate the extremely acute periphery of *Pleurotomaria perlata* and this character serves to distinguish Hall's species from *Isfarispira septata*. Whether or not *Pleurotomaria perlata* should be referred to *Isfarispira*, *Liospira* or another genus must remain an open question until better preserved material is described.

Preservation and variation in the material. The holotype of *Isfarispira septata* (Pl. 1, figs, 3, 7–8) is the most complete specimen, but the aperture is not preserved and the upper surface is eroded. Two septa are visible about one and three-quarter whorls back from the preserved aperture (point b in Pl. 1, fig. 8) and seem to

EXPLANATION OF PLATE 1

Figs 1–8. *Isfarispira septata* gen. et sp. nov.; Chorkuin Formation, Silurian; Central Asia. 1–2, CSGM 980*f*, paratype; locality 1974-1; × 1; 1, final whorl with spire broken away, in apical view to show the circumbilical flange; 2, in lateral view, the left margin of 1. 3, 7–8. CSGM 980*a*, holotype; locality PI-15; × 1; 3, umbilical view showing faint growth lines in the lower left quadrant; 7, apertural view showing the shallowly cyrtoconoid spire, which becomes concave with the transition to the last whorl, and the prominent septum (a) visible due to removal of parts of the upper surface by weathering; 8, apical view of the weathered specimen, note septa at b (probably marking the adapical termination of the body chamber), a (see also 7) and c. 4–6, CSGM 980*d*, paratype; locality 1974-1; internal mould; × 1; 4, transverse section (see also Text-fig. 2B) showing cyrtonconoid form of early whorls; 5, umbilical view showing sedimentary infill to the umbilicus at a stage when the circumbilical flange was not yet formed; 6, apical view.



GUBANOV *et al.*, *Isfarispira septata* gen. et sp. nov.

delimit the adapical termination of the body chamber; a fill of grey limestone occurs adaperturally of these septa, whereas red-stained carbonate (perhaps partly shell wall) occurs adapically of the pair of septa. A group of three septa spaced at 2–3 mm occurs about half a whorl earlier in ontogeny (point c in Pl. 1, fig. 8), and a single septum is also visible about half a whorl earlier still (Pl. 1, figs 7–8; point a). The presence of other septa cannot be ascertained because of the poor preservation of the upper surface.

Paratype CSGM 980*b* is an internal mould which has been transversely polished through the apex (Text-fig. 2A). The profile is gradate, but this is partly a result of weathering and of thickening of the now removed shell near the periphery of the whorl; septa are not visible. The circumbilical flange is well preserved and curves strongly from the base of the whorl in towards the axial region, where it becomes almost parallel to the axis of coiling. In the latest preserved whorls, sediment has penetrated into the spiral circumbilical cavity formed between the flange and the umbilical wall of the whorl, but this cavity is filled with calcite spar in earlier growth stages.

Paratype CSGM 980*c* (Text-figs 2C–D) is the only specimen available from locality 110A, and occurs in a separate nappe from the localities yielding the other specimens of *Isfarispira septata*. It is a badly weathered internal mould which has been ground down and polished to show a transverse section slightly oblique to the axis of coiling. It is proportionally taller than the holotype and preserves parts of eight whorls. Septa are clearly visible in intermediate growth stages but have not been observed in the earliest or latest growth stages. On account of the excentric section, the circumbilical flange appears to extend across the umbilicus, except at the latest growth stage where it is seen as a short blade protruding into the umbilicus; much of the shell at this growth stage seems to have been dissolved diagenetically. Calcite spar is conspicuous in the umbilicus and whorls at intermediate growth stages, but lime mud fills the latest whorls and also the early whorls. The distribution of lime mud in the early whorls indicates that the apex was perforated, either during or after the life of the gastropod, and that septa were not present or were secondarily destroyed in these early whorls.

Three paratypes were collected from locality 1974-1. One of these (specimen CSGM 980*d*; Pl. 1, figs 4–6; Text-fig. 2B) is a juvenile which has been transversely sectioned. The circumbilical flange is not developed in the final whorl and septa are not visible in the lime mud filling of the shell. A large, transversely sectioned specimen (CSGM 980*e*; not illustrated) shows distinct septa in intermediate growth stages but is too poorly preserved to assess the presence or absence of septa in the early growth stages. Specimen CSGM 980*f* is an internal mould of the final whorl showing the circumbilical flange clearly preserved on its upper surface (Pl. 1, figs 1–2).

MODE OF LIFE OF *ISFARISPIRA*

The lenticular form of *Isfarispira* combines a low spire and flattened base to produce a shell with a high surface area, when restored in the presumed living position with the lower surface lying on the sediment surface. The large surface area of the base counteracts sinking into soft bottom sediment and this snow-shoe effect is enhanced by other morphological co-adaptations. Notable amongst these is the shape of the whorl cross section, with maximum extent almost perpendicular to the axis of coiling and thus parallel to the sediment surface (cf. Text-fig. 2). In addition, the prominent circumbilical flange extends deep into the umbilicus to increase the area of shell in contact with the substrate and may serve to exclude sediment from the deeper parts of the umbilicus. Interpretation of the function of the flange is complicated, however, by consideration of its method of formation. Presumably, the flange was produced by an apertural extension of the mantle which partially, or completely, blocked the umbilicus at least during the period of secretion. The absence of the flange from the latest growth stage may indicate that this extension of the mantle was both extensive and possibly even a lasting feature. In such a case, the flange may have supported areas of soft tissue within the wide umbilicus near the aperture, or provided a smooth surface resting on an area of the foot extending beneath the shell in life.

The available small sample indicates quite substantial variation in the form of the circumbilical flange. In the specimen illustrated as Text-figure 2A, the flange is strongly curved and effectively delimits a spiral tube equivalent to the whorl, but located between the umbilical wall of the whorl and the upper surface of the flange. Sediment was probably largely excluded from this circumbilical tube during life. At the present time, the earliest growth stages are filled with calcite spar and sediment is restricted to the latest preserved growth stage. In other specimens, the circumbilical flange is less strongly curved and seems to have extended across the umbilicus towards the previous half whorl. Again, the presence of calcite spar filling the earliest growth stages may support the interpretation that the flange helped prevent sediment fill of the umbilicus.

Even the large number of whorls and the low rate of whorl expansion can be interpreted in relationship to the 'snow-shoe effect'. The surface area of the base of the shell is naturally increased by a high rate of growth (spiral shell accretion) and a high rate of whorl expansion, but the increase is counterbalanced by a corresponding increase in the volume of the soft parts. This effect is lessened, however, if the rate of growth of the shell, marked by its increase in surface area, is decoupled from the rate of growth of the soft parts. Thus, the low rate of whorl expansion in *Isfarispira* allowed the volume of the gastropod soft parts to increase more slowly than the rate of growth of the shell by spiral accretion, if the animal withdrew from the early part of the shell and lived only in the latest portion. The presence of septa in the interior of *Isfarispira* clearly demonstrates that the gastropod had withdrawn from the earlier (oldest) parts of the shell. In the holotype, septa are visible one and three-quarter whorls back from the aperture as preserved, delimiting the maximum extent of the body chamber. Thus, the earliest eight or more whorls were devoid of living tissue, being filled with water which probably had a slightly lower density than that of the soft parts. Withdrawal of the gastropod from the early whorls, in conjunction with the high rate of spiral growth and low rate of whorl expansion, enhanced shell growth at a minimum cost in terms of the energy requirements of the growing animal.

'Snow-shoe' adaptations are seen in a variety of other Palaeozoic and younger gastropods but different morphological solutions are employed from those described here in *Isfarispira*. Linsley *et al.* (1978) and Peel (1984*b*, 1986) discussed frilled Palaeozic gastropods. noting that the flange-like extension of the whorl periphery (as distinct from the flange extending into the umbilicus in *Isfarispira*) may have served either to prop the shell above a solid substratum, as in the recent *Xenophora*, or as a 'snow-shoe' to prevent sinking into soft sediment, as in the familiar Silurian *Euomphalopterus*. Peel (1977, 1978, 1984*b*, 1991*b*) suggested that the widely expanded aperture of certain Palaeozoic bellerophontacean gastropods represents expansion of the foot in response to life on a soft substratum. Other expanded bellerophontaceans, such as *Carinaropsis*, lack explanate margins and have thick shells (Peel 1993), indicating a limpet-like existence on harder substrates.

The presence of a radial aperture indicates that *Isfarispira* could not close its shell opening by clamping against the sediment. Shells with this apertural form are often sedentary or only occasionally mobile (Linsley 1977, 1978*b*) which accords well with the inferred 'snow-shoe' adaptation to life on a soft substrate. *Isfarispira* may have been a ciliary feeder or deposit feeder which only rarely moved to a new location. Some relatively thick-shelled Palaeozoic forms having this mode of life developed a prominent operculum (cf. Linsley and Yochelson 1972, Linsley 1978*a*), but it is not currently known if a calcified operculum was present in the thin-shelled *Isfarispira*. The presence of a calcified operculum and a thick shell tend to increase the specific gravity of the gastropod animal. The thin shell of *Isfarispira* and the eventual lack of a calcified operculum would have contributed to the 'snow-shoe' effect by keeping specific gravity to a minimum.

SEPTATION IN GASTROPODS

The presence of abundant internal septa in such disparate shell morphologies as the open coiled *Nevadaspira*, *Lytospira* and *Phanerotinus*, the thin-shelled and lenticular *Isfarispira*, the thick-shelled but low spired *Omphalocirrus* and *Hypomphalocirrus*, and the high spired *Fletcherviewia* suggests that septation in Palaeozoic gastropods is not associated with a particular mode of life or environment, although it is quite possible that this range of shell forms could have been found in gastropods feeding in a similar manner, for example by ciliary feeding, in different environmental settings.

We concur with Yochelson (1971) in his tentative dismissal of the idea that multiple septation could be a direct response to a need to strengthen the gastropod shell, as has been invoked within the Cephalopoda. Rather he suggested that withdrawal of soft parts 'may allow for greater efficiency in construction of the shell' (Yochelson 1971, p. 239) which, in general terms, agrees with the interpretation of the various shell features of *Isfarispira* presented here. Morris and Cleevely (1981) noted, without further discussion, that septation allowed withdrawal from, or loss of, the earliest whorls without inconvenience.

In *Isfarispira* it has been shown that withdrawal of the soft parts from the early whorls formed part of an adaptive strategy to life on a soft substrate by increasing the area of the resting surface of the gastropod relative to the volume of the soft parts (the 'snow-shoe' effect). A similar interpretation can be advanced for septation in *Nevadaspira*, *Lytospira* and *Phanerotinus*, but the operculate *Omphalocirrus* and *Hypomphalocirrus* have dissimilar, thick shells with more rapidly expanding whorls. In this case, withdrawal from the earliest growth stages may simply reflect a body mass of such a shape and size that it no longer required the narrow early whorls; in short, a slightly special case of the general withdrawal from the apical whorls typical of most gastropods. This may parallel the situation in the extant ciliary feeding vermetid *Dendropuma*, where the body mass is relatively short and plump and septa frequently close off earlier parts of the shell (Morton 1965).

Cook (1993) noted that *Fletcherviewia*, a high spired form with a thick shell and strongly angulated whorls, lived in high energy environments where the early whorls might be lost while the living shells were rolled along the substrate. Shortening of the body mass and secretion of septa closed off the early whorls which were susceptible to erosion and effectively prevented apical perforation of the shell. Cook (1993) supported his interpretation by reference to specimens lacking the apical portion and with the apex encrusted by calcareous algae, although such features also readily occur after death. Apical perforation may have occurred also in *Isfarispira*, since the earliest whorls in some specimens are filled with lime mud, while intermediate septate whorls are filled with calcite spar (Text-fig. 2c). In the interpreted soft-sediment environment, however, such perforation probably resulted from corrosion rather than erosion. Attempted predation may also produce perforation of the shell apex but durophagous predators at the present day mainly attack the aperture (Vermeij *et al.* 1980, 1981; Vermeij 1982, 1983, 1993). While shell boring predators are known from the latest Precambrian and Cambrian (Bengtson and Yue 1992; Conway Morris and Bengtson 1994), evidence of this and other forms of predation in the Palaeozoic is uncommon when compared with the Mesozoic and Cenozoic (Vermeij 1987). Published records of predation, or attempted predation, on gastropods in the Palaeozoic are rare, although undocumented cases are known to the authors. Peel (1984*c*) described shell repair in *Euomphalopterus* from the Silurian of Gotland which he attributed to repeated attempted predation. Rohr (1993) and Horny (1993) described cases of shell repair from the Ordovician and Devonian, respectively, which may have had a similar origin.

While septa in all these cases clearly serve to close off earlier (older) parts of the gastropod shell, the causes for withdrawal of soft parts from the early shell are different. Thus, septation provides no single diagnostic character in terms of the mode of life of septate Palaeozoic gastropods, but represents one among many shell features developed in response to varied adaptive strategies.

Acknowledgements. A research grant from the Swedish Natural Science Research Council (NFR) to JSP allowed APG to bring the material described in this paper to Uppsala for study and description. Photographs were taken by Olga Uljanova, Novosibirsk. Enrico Savazzi, Uppsala, is thanked for discussion of the material and of the manuscript.

REFERENCES

BASSLER, R. S. 1915. Bibliographic index of American Ordovician and Silurian fossils. *Bulletin of the US National Museum*, **92**, 1521 pp.

BENGTSON, S., CONWAY MORRIS, S., COOPER, B. J., JELL, P. A. and RUNNEGAR, B. 1990. Early Cambrian fossils from South Australia. *Memoir of the Australasian Association of Palaeontologists*, **9**, 364 pp.

—— and YUE ZHAO 1992. Predatorial borings in late Precambrian mineralized exoskeletons. *Science*, **257**, 367–369.

CONWAY MORRIS, S. and BENGTSON, S. 1994. Cambrian predators: possible evidence from boreholes. *Journal of Paleontology*, **68**, 1–23.

COOK, A. G. 1993. *Fletcherviewia septata*: a new high-spired, septate gastropod from the Devonian of North Queensland. *Journal of Paleontology*, **67**, 816–821.

CUVIER, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. Paris, 710 pp.

FISCHER, D. W. 1962. Small conoidal shells of uncertain affinities. W98–W143. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part W. Miscellanea.* Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 259 pp.

HALL, J. 1852. *Palæontology of New-York. Vol. II. Containing descriptions of the organic remains of the lower middle division of the New-York System, (equivalent in part to the middle Silurian rocks of Europe)*. Charles Van Benthuysen, Albany, 362 pp.

HORNY, R. J. 1993. Shell morphology and mode of life of the Lower Devonian cyclomyan *Neocyrtolites* (Mollusca, Tergomya). *Časopis Národního Muzea Praha*, **162**, 57–66.

KNIGHT, J. B. 1941. Paleozoic gastropod genotypes. *Geological Society of America, Special Paper*, **32**, 510 pp.

—— 1945. Some new genera of Paleozoic Gastropoda. *Journal of Paleontology*, **19**, 473–587.

—— COX, L. R., KEEN, A. M., BATTEN, R. L., YOCHELSON, E. L. and ROBERTSON, R. 1960. Systematic descriptions [Archaeogastropoda], I169–I310. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part I. Mollusca 1.* Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 351 pp.

KOKEN, E. and PERNER, L. 1925. Die Gastropoden des baltischen Untersilurs. *Mémoire de l'Académie des Sciences de Russie, VIII série, Classe Physico-mathématique, Leningrad*, **37**, 1–326.

KONINCK, L. G. de 1881. Faune du calcaire carbonifière de la Belgique. *Annales de Musée Royal d'Historie Naturelle de Belgique, Série Paléontologique*, **6**, 1–170.

LINDSTRÖM, G. 1884. On the Silurian Gastropoda and Pteropoda of Gotland. *Kongliga svenska Vetenskaps-Akademiens handlingar*, **19**, 250 pp.

LINSLEY, R. M. 1977. Some 'laws' of gastropod shell form. *Paleobiology*, **3**, 196–206.

—— 1987*a*. The Omphalocirridae: a new family of Palaeozoic Gastropoda which exhibits sexual dimorphism. *Memoir of the National Museum of Victoria*, **39**, 33–54.

—— 1978*b*. Shell form and evolution of the gastropods. *American Scientist*, **66**, 432–441.

—— and YOCHELSON, E. L. 1972. Opercula of two gastropods from the Lilydale Limestone (Early Devonian) of Victoria, Australia. *Memoir of the National Museum of Victoria*, **33**, 1–14.

—— YOCHELSON, E. L. and ROHR, D. M. 1978. A reinterpretation of the mode of life of some Palaeozoic frilled gastropods. *Lethaia*, **11**, 105–112.

MILNE EDWARDS, H. 1848. Note sur la classification naturelle des mollusques gastéropodes. *Annales de la Science Naturelle, Zoologique, Série 3*, 102–112.

MIRONOVA, L. G. 1993. [Klass Gastropods – bruchonogi molluski.] 5–10. *In* KISELEV, G. N. (ed.). *V knige Atlas molluskoi i brachiopod silura i devona uzhnogo Tyan-Chanya. Izdatelstvo Sankt-Peterburskogo Universiteta*, 73 pp. [In Russian].

MORRIS, N. J. and CLEEVELY, R. J. 1981. *Phanerotinus cristatus* (Phillips) and the nature of euomphalacean gastropods. *Bulletin of the British Museum (Natural History), Geology Series*, **35**, 195–212.

MORTON, J. E. 1965. Form and function in the evolution of the Vermetidae. *Bulletin of the British Museum (Natural History), Zoology Series*, **2**, 586–630.

PEDDER, A. E. H. 1966. The Upper Devonian gastropod *Orecopia* in western Canada. *Palaeontology*, **9**, 142–147.

PEEL, J. S. 1977. Systematics and palaeontology of the Silurian gastropods of the Arisaig Group, Nova Scotia. *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, **21**, 1–89.

—— 1978. Faunal succession and mode of life of Silurian gastropods in the Arisaig Group, Nova Scotia. *Palaeontology*, **21**, 285–306.

—— 1984*a*. Autecology and systematics of a new Silurian anomphalid gastropod from western North Greenland. *Grønlands Geologiske Undersøgelse, Rapport*, **121**, 77–87.

—— 1984*b*. Autecology of Silurian gastropods and monoplacophorans. *Special Papers in Palaeontology*, **32**, 165–182.

—— 1984*c*. Attempted predation and shell repair in *Euomphalopterus* (Gastropoda) from the Silurian of Gotland. *Bulletin of the Geological Society of Denmark*, **32**, 163–168.

—— 1986. Systematics and mode of life of a new Silurian *Clisospira* (Mollusca) from North Greenland. *Grønlands Geologiske Undersøgelse, Rapport*, **128**, 65–74.

—— 1991*a*. The Classes Tergomya and Helcionelloidea, and early molluscan evolution. *Bulletin of the Grønlands Geologiske Undersøgelse*, **161**, 11–65.

—— 1991*b*. *Salpingostoma* and related bellerophontacean gastropods from Greenland and the Baltic region. *Bulletin of the Grønlands Geologiske Undersøgelse*, **161**, 67–116.

PEEL, J. S. 1993. Muscle scars and mode of life of *Carinaropsis* (Bellerophontoidea, Gastropoda) from the Ordovician of Tennessee. *Journal of Paleontology*, **67**, 528–534.
—— and YOCHELSON, E. L. 1976. Two new gastropod genera from the Lower Silurian of the Oslo Region, Norway. *Norsk Geologisk Tidsskrift*, **56**, 15–27.
RASETTI, F. 1957. Additional fossils from the Middle Cambrian Mt Whyte Formation of the Canadian Rocky Mountains. *Journal of Paleontology*, **31**, 955–972.
ROHR, D. M. 1993. Middle Ordovician carrier shell *Lytospira* (Mollusca, Gastropoda) from Alaska. *Journal of Paleontology*, **67**, 959–962.
THIELE, J. 1925. *Mollusca = Weichtere: Handbüch der Zoologie, gegründet W. Kükenthal* 5. *Fischer, Berlin and Leipzig*, 258 *pp*.
ULRICH, E. O. and SCOFIELD, W. H. 1897. The Lower Silurian Gastropoda of Minnesota. *Geology of Minnesota. Final Report of the Geological Survey of Minnesota*, **32**, 813–1081.
VERMEIJ, G. J. 1982. Gastropod shell form, repair, and breakage in relation to breakage by the crab *Calappa*. *Malacologia*, **23**, 1–12.
—— 1983. Traces and trends in predation, with special reference to bivalved animals. *Palaeontology*, **26**, 455–465.
—— 1987. *Evolution and escalation*. Princeton University Press, Princeton, New Jersey, 527 pp.
—— 1993. *A natural history of shells*. Princeton University Press, Princeton, New Jersey, 207 pp.
—— SCHINDEL, D. E. and ZIPSER, E. 1981. Predation through geological time: evidence from gastropod shell repair. *Science*, **214**, 1024–1026.
—— ZIPSER, E. and DUDLEY, E. C. 1980. Predation in time and space: peeling and drilling in terebrid gastropods. *Paleobiology*, **6**, 352–364.
WEBERS, G. F., POJETA, J. Jr and YOCHELSON, E. L. 1992. Cambrian Mollusca from the Minaret Formation, Ellsworth Mountains, West Antarctica. *Memoir of the Geological Society of America*, **170**, 181–248.
WHITEAVES, J. F. 1884. On some new, imperfectly characterized, or previously unrecorded species of fossils from the Guelph formation of Ontario. *Geological Survey of Canada, Palaeozoic Fossils*, **3**, 1–43.
—— 1906. Revised list of the fossils of the Guelph formation of Ontario. *Geological Survey of Canada, Palaeozoic Fossils*, **3**, 327–340.
WILLIAMS, M. Y. 1919. The Silurian geology and faunas of the Ontario Peninsula, and Manitoulin and adjacent islands. *Memoir of the Geological Survey of Canada*, **111**, 1–193.
YOCHELSON, E. L. 1966. A reinvestigation of the Middle Devonian gastropods *Arctomphalus* and *Omphalocirrus*. *Norsk Polarinstitutt, Årbok 1965*, 37–48.
—— 1971. A new Upper Devonian gastropod and its bearing on open coiling and septation. *Smithsonian Institution, Contributions in Paleobiology*, **3**, 231–241.
—— FLOWER, R. H. and WEBERS, G. F. 1973. The bearing of the new Late Cambrian monoplacophoran genus *Knightoconus* upon the origin of the Cephalopoda. *Lethaia*, **6**, 275–310.

A. P. GUBANOV
Institute of Geology
Novosibirsk 630090, Russia

J. S. PEEL
Institute of Earth Sciences
Department of Historical Geology and Palaeontology
Uppsala University, Norbyvägen 22
S-752 36 Uppsala, Sweden

I. A. PIANOVSKAYA
Institute of Mineral Resources
13A Shevshenko
Tashkent 700060, Uzbekistan

Typescript received 3 January 1995
Revised typescript received 7 April 1995