

SINISTRAL HYPERSTROPHIC COILING IN A DEVONIAN GASTROPOD FROM BOHEMIA WITH AN *IN SITU* OPERCULUM

by JOHN S. PEEL *and* RADVAN J. HORNÝ

ABSTRACT. A paucispiral operculum is described *in situ* in a specimen of *Tychobrahea aerumnans* from the Devonian of Bohemia. The small turbiniform gastropod shell appears to be dextrally orthostrophically coiled in similar fashion to most other fossil and extant gastropod shells, but the clockwise-coiling of the exterior surface of the operculum indicates that coiling of the shell is sinistral hyperstrophic. This is the first description of an operculate gastropod with this type of coiling in the fossil record.

To most people, a conispiral shell is the characteristic feature of gastropod molluscs, although this type of coiling into a three-dimensional spire is neither restricted to the class nor diagnostic of it. Rather, gastropods are distinguished by having undergone torsion at some stage in their developmental or evolutionary history, a process involving rotation of the originally posterior mantle cavity to an anterior position. The gut and visceral loop become twisted and the anatomy of the gastropod is profoundly asymmetrical (Cox 1960). Torsion is anti-clockwise in the vast majority of living gastropods and the paired organs associated with the originally posterior mantle cavity are reduced or lost in most gastropods on the post-torsional right side, when viewed from above. Such a gastropod can be described as anatomically dextral; anatomical sinistrality involves clockwise torsion and reduction of organs on the post-torsional left side (Robertson 1993).

Torsion and the resultant asymmetry of the soft parts have been considered to be closely related to the conispiral coiling of most gastropod shells (cf. Knight 1952; Pojeta and Runnegar 1976; Linsley 1978*a*; Lever 1979; Robertson 1993). Conispiral coiling, however, is also developed in untorted molluscs such as the onychochilid paragastropods (Linsley and Kier 1984) and the Pelagiellidae (cf. Peel 1992). On the other hand, many limpet gastropods show a high degree of bilateral symmetry in the adult shell while the soft parts are conspicuously asymmetrical (Fretter and Graham 1994). Changes in the form and orientation of conispiral shells are closely linked to anatomical adaptation and evolution of the gastropod animal. Re-orientation of the shell and associated morphological change are two of the most conspicuous trends in gastropod evolution (Linsley 1978*a*, 1978*b*).

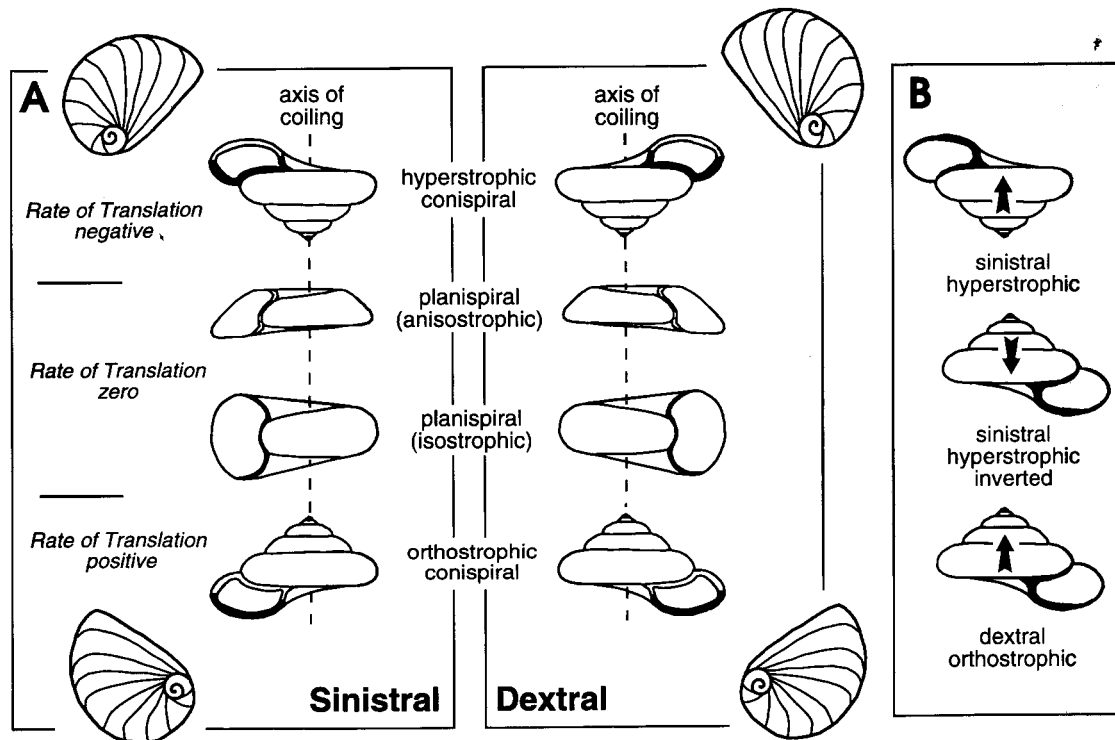
The terms dextral and sinistral are most commonly applied to the direction of coiling of gastropod shells. Most gastropod shells are coiled dextrally when viewed in standard orientation, i.e. the aperture lies to the right of the axis of coiling when the shell is placed with the aperture facing the viewer, with the apex uppermost and the axis of coiling vertical (Text-fig. 1). In apical view, such a shell increases in a clockwise direction with the addition of successive increments of growth. A mirror image of a dextral shell produces a form in which the aperture lies to the left of the axis in apertural view, and this sinistral shell increases in an anti-clockwise spire when viewed apically.

Sinistral coiling is much less common than dextral coiling within the Gastropoda but it is widespread, particularly within pulmonates (Vermeij 1975, 1993; Robertson 1993). Sinistral species or genera, such as the familiar *Neptunea contraria* or *Sinistrofulgur sinistrum*, occur in many groups and at least one marine family with an extensive fossil record, the Amberleyidae, contains a conspicuous number of sinistral forms (cf. Knight *et al.* 1960; Vermeij 1993). Sinistral individuals

sometimes occur as rare mutations within otherwise dextral populations (cf. Gould 1993, p. 452; Robertson 1993, figs 14–17).

Sinistral and dextral shells need not be conspiral. If the rate of translation (parameter T of Raup 1966) of the whorl along the axis of coiling with growth is zero, the resultant shell form is planispiral with coiling within a single plane. Most planispiral gastropod shells are conspicuously anisotropic, enabling easy recognition of the type of coiling. If the shell is isotropic, however, and bilaterally symmetrical about a plane perpendicular to the axis of coiling, the form of the shell alone offers no clue concerning the direction of coiling. Isotropic coiling is characteristic of bellerophontoidean gastropods which were prominent in the Palaeozoic.

If the rate of translation (T) of the whorl is negative the shell can be considered to grow up its axis of coiling relative to the normal condition where T is positive and the shell grows down the axis. Such shells with negative translation are termed hyperstrophic while positive translation produces orthostrophic coiling (Text-fig. 1A). In a hyperstrophic shell, the whorls are extended into a basal



TEXT-FIG. 1. A, coiling patterns in gastropod shells comparing orthostrophic and hyperstrophic coiling in sinistral and dextral morphologies, together with schematic illustrations of associated opercula (viewed from the exterior). Equivalent areas of the shell aperture in orthostrophic and hyperstrophic conspiral shells are coloured black, B, identity in shell form between sinistral hyperstrophic coiling and the dextral orthostrophic coiling which is overwhelmingly dominant within the Gastropoda. These two morphologies can only be separated by study of soft anatomy or by comparing the coiling directions of the shells with their respective opercula. Arrows indicate 'up' in standard orientation.

spire equivalent to the lower surface (base) of the orthostrophic shell in standard orientation, and not to the extended orthostrophic spire. Dextral and sinistral morphologies are geometrically possible within both orthostrophic and hyperstrophic shells. Dextral and sinistral morphotypes are essentially mirror images of each other, also in terms of anatomy, but no similar relationship exists

between the orthostrophic and hyperstrophic forms (Text-fig. 1B). Anatomical dextrality is present in gastropods with dextral orthostrophic and dextral hyperstrophic shells, the latter case giving rise to the description of anatomically dextral gastropods in apparently sinistral shells.

Comparison of the shell morphologies illustrated in Text-figure 1 reveals a conchological dilemma, for it is evident that a dextral orthostrophic shell may be morphologically indistinguishable from a sinistral hyperstrophic shell (and a sinistral orthostrophic from a dextral hyperstrophic) even though equivalent areas of the whorl profile are located at different locations within the shell viewed as a whole. In the living gastropod the issue can be resolved by reference to soft anatomy but this approach fails in the fossil record. Analysis of shell features such as apertural shape may provide useful clues in unusual morphologies (cf. Linsley and Kier 1984) but the student of fossil gastropods will usually describe a shell in terms of orthostrophic coiling, mainly on the basis of the knowledge that hyperstrophic coiling is very rare at the present day (Robertson 1993).

One shell feature capable of preservation in the fossil record provides irrefutable evidence concerning direction of coiling, namely the direction of coiling of the spiral operculum (there are also opercula which grow by concentric growth (cf. Yochelson 1990; Gubanov and Yochelson 1994). When viewed externally, spiral gastropod opercula coil in the opposite direction to the direction of coiling of the shell, as a function of the addition of consecutive growth increments of the operculum at the parietal margin of the aperture (Hickman and McLean 1990). Thus, the outer surface of the operculum is coiled sinistrally (anti-clockwise) in a dextrally coiled orthostrophic shell but dextrally (clockwise) in a sinistrally coiled orthostrophic form (Text-fig. 1). The operculum is also sinistral in a dextral hyperstrophic shell viewed in the correct orientation, with the basal spire down. If the shell is incorrectly interpreted as sinistral orthostrophic, however, and oriented with the basal spire pointing up, the operculum will be coiled in the same direction as the shell.

Most living shell-bearing gastropods possess an operculum at some stage in their development. Isolated opercula (Pl. 1, fig. 1) are well known as fossils within the Palaeozoic but are usually uncommon (Yochelson 1979). Records of fossil gastropod shells with the operculum preserved *in situ* within the shell aperture are few (e.g. Perner 1903, 1907, 1911; Teller 1910; Knight 1941; Boucot *et al.* 1966; Yochelson and Linsley 1972; Yochelson and Wise, 1972; Linsley 1978c; Yochelson 1990; Gubanov and Yochelson 1994). Lindström (1884, pl. 17; see also Peel 1984) illustrated opercula *in situ* in *Oriostoma cornuta* and *O. globosa* and a variety of isolated opercula from the Silurian of Gotland, Sweden. Several of the described associations of operculum and shell have enabled important re-interpretation of the nature of coiling of the host shell. Thus, the widespread and abundant Ordovician *Maclurites* is interpreted as dextral hyperstrophically coiled rather than sinistral orthostrophic on the basis of its operculum (Knight *et al.* 1960; Rohr 1979; Yochelson 1979), although Yochelson (1990) reviewed this interpretation of the operculum. Similarly, Linsley (1978c) demonstrated that Devonian omphalocirrids were dextral rather than sinistral on the basis of finds of *in situ* opercula.

In the present paper we describe a unique specimen of the gastropod *Tychobrahea aerumnans* Horný, 1992 from the Devonian of Bohemia in which the operculum is preserved essentially *in situ* within the aperture. This specimen is of particular interest in that the direction of coiling of the operculum demonstrates that the Bohemian gastropod was sinistral hyperstrophic rather than dextral orthostrophic, as cursory examination of the conispiral shell might suggest. This is the first report of this exceptional type of coiling in marine gastropods in the fossil record. Sinistral hyperstrophic occurs in many planorboid gastropods but these freshwater pulmonates lack an operculum, and characteristically have an almost planispiral shell.

SYSTEMATIC PALAEOONTOLOGY

Tychobrahea aerumnans Horný, 1992

Plate 1, figures 2–5, 8

1992 *Tychobrahea aerumnans* Horný, p. 104, pl. 3, figs 1–4.

Description. Only one specimen with the operculum preserved *in situ*, but slightly displaced, has been found among many hundreds of isolated specimens of this species collected from various Lower Devonian micritic limestones in the vicinity of Prague. Horný (1992) designated this specimen as the holotype of *Tychobrahea aerumnans*. It is an almost complete shell, isolated from weathered and washed limestone, and it is preserved as recrystallized calcite. It was collected by the late F. Hanuš from the 'Red Quarry' near Klukovice, Prague, in the Pragian (Lower Devonian) Dvorce-Prokop Limestone.

The holopeiform shell is regularly coiled, originally with weak prosocline growth lines. The whorls are slightly shouldered but the angulation is not reflected on the internal shell surface. The base is rounded, anomphalous, with the umbilical region partly filled with a thick, crescent-like, flattened columellar callus. The shell wall forming the apertural margin slopes adapically in towards the shell interior with shallow convexity from the acute outer margin; the internal profile of the aperture is almost circular. The shell is thick, thinnest in the parietal region.

The operculum is preserved within the entrance of the last whorl; it has been pressed in obliquely and slightly rotated after death. On account of this oblique orientation, it is possible to observe both the external surface and the lateral profile of the operculum. The inner surface of the operculum has been cemented to the internal shell wall and partly covered by the shell of a tentaculite. The outer surface of the operculum is more intensely weathered than the shell with corrosion mainly following the opercular sutures, an observation also made by Yochelson and Linsley (1972) in *Cyclonema lilydalense* from the lowermost Devonian of Australia.

The operculum is almost circular, relatively massive and thick (about 0.35 mm at the periphery, compared with the thickness of the shell itself, 0.25 mm, at the aperture below the periphery; the total height of shell is 6.8 mm). The operculum is completely recrystallized, translucent, with no traces of growth increments. In profile, the edge of the operculum is concave, sloping in towards the shell interior such that the diameter of the outer surface of the operculum is larger than the diameter of the inner surface. This lateral margin of the operculum corresponds in shape to the bevelled edge of the aperture, although the operculum in the available specimen is withdrawn slightly into the aperture. The outer surface clearly demonstrates that the operculum is paucispiral, regularly and slowly expanding in a clockwise direction (Pl. 1, fig. 2). The rate of rotation corresponds approximately to the growing rate of the shell; the angle of accretion is high, approximately 90 degrees. The outer surface of the operculum is generally flat but, as mentioned above, corrosion has emphasized the opercular sutures. The latest preserved volution is slightly concave medially but the coarse preservation obscures the nature of the earliest growth stages. The internal surface of the operculum is not visible.

Some doubt exists concerning the position of the accreting zone of the operculum relative to the shell. At the present time, the accreting margin faces the columellar lip. The internal profile of the aperture is circular, however, making it difficult to restore the operculum to its original position.

Occurrence and associated fauna. *Tychobrahea aerumnans* is one of the most abundant gastropods within the Lower Devonian of Bohemia (Horný 1992). These morphologically variable, thick-shelled gastropods, possible sedentary suspension feeders, were seemingly quite successful in the low energy conditions prevalent during the Early Devonian and represented by micritic limestone facies. *T. aerumnans* is totally absent from the

EXPLANATION OF PLATE 1

Fig. 1. External view of an isolated paucispiral operculum, probably of *Australonema* cf. *guillieri* (Oehlert), from the Lower Devonian (Pragian), Koněprusy Limestone, Koněprusy, Bohemia (after Horný 1994); National Museum, Prague, L 8764; the operculum is coiled in an anti-clockwise spiral, indicating that the host gastropod shell was dextral orthostrophic; $\times 8$.

Figs 2–5, 8. *Tychobrahea aerumnans* Horný, 1992, Lower Devonian (Pragian), Dvorce-Prokop Limestone, Praha-Klukovice, Bohemia; National Museum, Prague, L 29194; holotype. 2, oblique view of the aperture and the upper surface showing the clockwise coiling of the outer surface of the operculum; $\times 15$. 3–5, three different apertural views oriented as a sinistral hyperstrophic gastropod with the operculum *in situ*. Note that the operculum is slightly displaced so that its concave lateral margin is visible in 5; $\times 11$. 8, the same specimen in apertural view, but oriented as a dextral orthostrophic gastropod; $\times 11$.

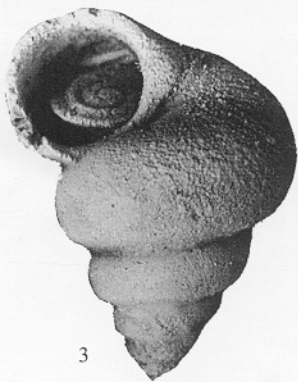
Figs 6–7. *Tychobrahea* aff. *T. aerumnans* Horný, 1992; lateral and oblique apertural views showing a prominent callus in the umbilical region; Lower Devonian (Dalejan), Třebotov Limestone, Praha-Holyně, Bohemia; National Museum, Prague, L 29233; $\times 11$.



1



2



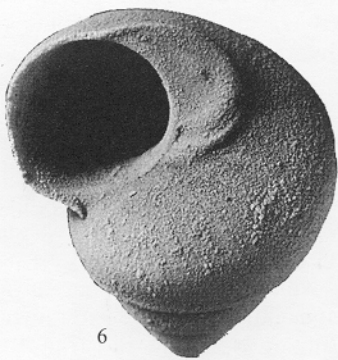
3



4



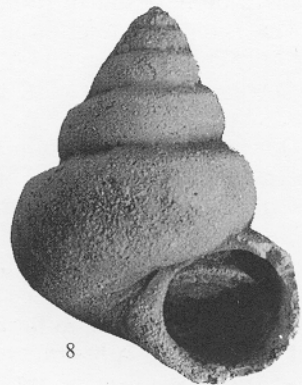
5



6



7



8

Koněprusy bioherm and its surroundings. In contrast with other contemporaneous gastropods within the low energy environments, such as *Hanusispira*, *Palaeozygopleura* and *Diplozone*, *T. aerumnans* is extremely variable. According to Horný (1992), this variability is mainly expressed in the height of the shell, presence or absence of an umbilicus, the profile of the upper part of the whorl (whether gradate or rounded) and the degree of development of the columellar callus. Other co-occurring gastropods, especially the loxonemataceans and pleurotomariaceans, frequently show evidence of shell repair, but repaired injuries have not been observed in *T. aerumnans*.

Associated gastropods include *Tropidodiscus*, *Kodymites*, *Paleuphemites*, *Trochoclisia*, *Straparollus*, *Ptychomphalina*, *Hanusispira*, *Pragoloron*, *Umbotropis*, *Vladanella*, *Dongiovannia*, *Oriostoma*, *Naticopsis*, *Diplozone*, *Loxonema*, *Katoptychia*, *Palaeozygopleura* and subulitids, all associated with a diverse invertebrate fauna. The low energy environment was dominated by deposition of soft calcareous mud, microbioclastic material (mainly crinoidal) and diffuse organic matter. A unifying theme within the whole fossil assemblage is small size (with the exception of local accumulations of large trilobite carapaces). Noteworthy, is the rare occurrence of dwarfed specimens of gastropods, such as *Platyceras* (*Praenatica*), which reach their normal size in the reef facies some 30 km to the west. All washed samples contain a high percentage of undamaged juvenile gastropod shells, together with tiny remains of echinoderms, holothuroid plates and foraminifers, but isolated gastropod opercula are lacking.

THE QUESTION OF HYPERSTROPHY

It is a character of spiral gastropod opercula, when viewed externally, that they are coiled in the opposite direction to the coiling of the shell (Cox 1960; Yochelson and Linsley 1972; Linsley and Kier 1984; Robertson 1993). Thus, as noted above, in a typical dextral orthostrophic gastropod viewed from the apex, coiling is clockwise and the operculum is coiled anti-clockwise when viewed from the exterior (Pl. 1, fig. 1). When viewed from the internal surface, the coiling of the same operculum is clockwise.

The operculum in *Tychobrahea aerumnans* is coiled clockwise on the outer side as preserved (Pl. 1, fig. 2) which indicates that the shell is coiled anti-clockwise, i.e. sinistrally. Clearly, the shell appears to be dextral (with the aperture at the right) when viewed in standard orientation (Pl. 1, fig. 8) whereas the aperture would lie to the left in a sinistral form. This apparent incongruity is resolved by interpreting the shell of *T. aerumnans* as hyperstrophic. Oriented as a sinistral hyperstrophic gastropod and viewed from the upper umbilical surface (Pl. 1, fig. 2), *T. aerumnans* is coiled anti-clockwise while the operculum is coiled clockwise, satisfying the relationship between shell and operculum noted above. A similar argument has been presented by Linsley (1978c) in his interpretation of the orientation of omphalocirrid shells, although in this case he demonstrated that shells widely presumed to be sinistral were dextral, on the basis of their operculum.

This is the first description of a fossil marine gastropod interpreted as sinistral hyperstrophic and the only described example of an operculum in such a shell form. On account of our assertion, and the rarity of hyperstrophic gastropods at the present day (cf. Linsley and Kier 1984; Robertson 1993; Vermeij 1975, 1993), it is prudent to scrutinize the claim closely.

Our interpretation assumes that the relationship between coiling in the gastropod shell and in the operculum is constant. This relationship was questioned by Rohr and Boucot (1985) while describing isolated opercula from the Lower Silurian of Quebec. They described anti-clockwise coiling on both the inner and outer surfaces of *Oriostoma* opercula when viewed from the respective surface, an observation which requires the inner and outer surfaces to grow in opposite directions. Coiling on the outer surface of the opercula, however, is multispiral while that on the inner surface is paucispiral. Rohr and Boucot (1985) proposed that the anomalous coiling on the interior surface was an artefact possibly resulting from a migrating muscle. Similar opercula illustrated by Lindström (1884) from the Silurian of Gotland appear to support this interpretation and there is little reason to doubt that the familiar association of anti-clockwise opercula (when viewed externally) and a dextral orthostrophic shell is correct (cf. Lindström 1884; Peel 1984).

Incidentally, Gubanov and Yochelson (1994) cited Rohr and Boucot (1985) in interpreting an association of a gastropod and operculum described by Teller (1910) from the Silurian of Wisconsin under the name *Murchisonia conradi*. Similar opercula from the same horizon and general locality

were illustrated by Peel (1987, fig. 14.30c). Teller's (1910, pl. 150, fig. 1) illustration indicates an external mould of the gastropod and an operculum which, as preserved, is coiled in a clockwise direction. Teller (1910) considered the illustration to represent an impression of the outer surface of the operculum. Thus, the operculum itself would be coiled in an anti-clockwise direction when viewed externally. This would indicate a dextral shell which seems to agree with Teller's (1910) illustration, where the apparent sinistrality of the dextral shell results from its orientation with the aperture facing away from the observer. Gubanov and Yochelson (1994) considered Teller's fossil to represent an imprint of the paucispiral inner surface of a multispiral operculum of *Oriostoma*-type such as described by Rohr and Boucot (1985) but the location of the operculum relative to the gastropod shell in Teller's (1910) illustration would imply that *M. conradi* is truly sinistral if this interpretation is correct. This does not appear to be the case but this enigmatic association requires re-description.

The resemblance between illustrations of Teller's (1910) operculum and the operculum of *T. aerumnans* is striking. Notwithstanding the conflicting interpretations, the Wisconsin specimens are undoubtedly external moulds and coiling would be in the opposite direction in the operculum itself, opposite also to that in *T. aerumnans*.

If the presumed outer surface of the operculum in *T. aerumnans* was in fact an internal surface, and the operculum had been post mortally overturned such that the visible outer surface was the true inner surface, it would be possible to interpret *T. aerumnans* as a 'normal' dextral orthostrophic gastropod. Lindström (1884, p. 176) reported an operculum which he interpreted as overturned in a Silurian gastropod from Gotland but provided no illustration. This interpretation of *T. aerumnans* is countered by examination of the lateral margins of the operculum; these clearly slope inwards, with the currently visible outer surface being wider than the inner surface (Pl. 1, fig. 5). In addition, the lateral margins of the operculum are concave, producing a truncated conical form consistent with the function of the operculum as a lid to the shell aperture (cf. Linsley 1978c, pl. 10, figs 13, 16). Isolated Silurian opercula illustrated by Lindström (1884, pl. 17) are also conical, but the convex sides and the beehive form of the external surface show no similarity to the operculum of *Tychobrahea*. Thus, it is unlikely that the presumed outer surface of the operculum of *T. aerumnans* has been incorrectly identified.

The operculum in *T. aerumnans* appears to be smaller than the outer margin of the aperture (as preserved, it is withdrawn within the margin of the aperture; see Pl. 1, figs 2–5). This is a common feature of opercula in living gastropods (cf. Hickman and McLean 1990, fig. 1) and the operculum functions equally well as a protective lid if withdrawn from the outermost margin of the aperture. Deep placing of the operculum also provides added protection against predators which break back the apertural margins as a means of gaining access to the soft parts. It also allows the operculum to be opened slightly for respiration without extension beyond the protective apertural margins.

We cannot fully discount the possibility that an isolated operculum has been placed by chance within the aperture of another gastropod which fortuitously has the same apertural shape and general size as that from which the operculum was originally derived. Such cruel irony would permit the interpretation that the operculum is derived from a sinistral orthostrophic gastropod or a sinistral hyperstrophic gastropod and that it has subsequently been placed within the aperture of a dextral gastropod; the idea is rejected.

Linsley and Kier (1984) proposed a class Paragastropoda to include a number of apparently sinistral untorted molluscs which otherwise have been interpreted as hyperstrophic gastropods (Knight *et al.* 1960). A variety of forms – pelagiellids, onychochilids, macluritids and euomphalids(?) – were included within the class, although the authors accepted that their concept of Paragastropoda was a grade of organization rather than a single clade. A discussion of the scope of the class lies outside the present context but their proposal is relevant since some of the more familiar operculum-bearing gastropods of other authors, e.g. *Maclurites*, *Palliseria*, *Teiichispira*, *Omphalotrochus*, were included within the Paragastropoda. Linsley and Kier (1984) interpreted the relative orientation of gastropod and shell in the same way as if these supposed paragastropod molluscs were true gastropods.

Yochelson (1990) pointed out that the operculum in *Maclurites* grew by accretion around the entire margin and not just at a narrow growth zone, as is the case with spiral opercula (cf. Hickman and McLean 1990). Such a relationship is also evident in opercula of *Ceratopea* which are locally abundant in the Lower Ordovician of Laurentia (Yochelson 1979). The continuous spiral rotation of paucispiral and multispiral opercula with growth and the deposition of sequential growth increments at the parietal wall require that the interior of the aperture is almost circular in cross section, as in *T. aerumnans* (see also *Liomphalus northi* as illustrated by Yochelson and Linsley 1972, pl. 2, figs 1–5; Linsley 1978c, pl. 10, figs 13, 16; Peel 1987, fig. 14.30A). The angulation on the shell exterior in *T. aerumnans* is of no consequence, as it is not reflected on the shell interior. Spiral growth of a tightly fitted operculum with this degree of spiral rotation is not possible within the polygonal aperture of *Maclurites* and *Ceratopea* and growth occurs around the entire margin of the operculum, but not equally. Opercula of *Maclurites* and *Ceratopea* are still coiled, however, due to the differential growth at the opercular margin. This anti-clockwise curvature of the exterior surface of the operculum in *Maclurites* supports interpretation of the shell as dextral hyperstrophic, although strong evidence for this interpretation also lies in functional morphological interpretation of the shell alone. *Maclurites* undoubtedly followed a sedentary existence with its flattened lower surface in direct contact with the substrate; the hyperstrophic coiling of the shell reflects the influence of the surface upon which the probably filter feeding gastropod lived.

Onychochilid paragastropods are commonly more relatively high spired than most of the generally low spired operculum-bearing forms mentioned above but they show a range of shell morphologies quite unlike that seen in *T. aerumnans*. Onychochilid opercula are not known, although Linsley and Kier (1984) expected that they existed. We find little reason to interpret *T. aerumnans* as an onychochilid paragastropod despite our suggestion that it is hyperstrophically coiled. Moreover, sinistral hyperstrophy is not a known feature of paragastropods or gastropods, with the exception of the low spired planorbioids. Indeed, without evidence from the operculum, the condition is hardly recognizable in fossil material.

At the present day sinistral hyperstrophy is known only within the freshwater pulmonate Planorbioidea which lack an operculum and display anatomical sinistrality in an almost planispiral, slightly hyperstrophic shell (Robertson 1993). The most familiar example is perhaps *Carinifex newberryi* from western North America (cf. Robertson 1993, fig. 21) but planorbioids have a geological record extending back to the Jurassic (Tracey *et al.* 1993). Hyperstrophic coiling also occurs in the larval stages of shelled opisthobranchs, most architectonicid prosobranchs and in some freshwater snails (Robertson 1993) but adults revert to orthostrophy. *Lanistes* retains dextral hyperstrophy into adulthood.

Recognition of the sinistral hyperstrophic form of *T. aerumnans* complicates interpretation of its systematic position. It is not possible to decide if the coiling pattern is typical of the species or genus alone, or whether it is a character of a higher taxon. It is also possible that the single specimen with the operculum in place is sinistral hyperstrophic and most other individuals were dextral orthostrophic. By comparison, in the family Ampullariidae, some genera are dextral conispiral, others are planispiral while the genus *Lanistes* is hyperstrophic (Cox 1960). The shell of *T. aerumnans* itself shows some similarity to members of the family Holopeidae, but typical representatives of this family are thin-shelled and without a columellar callus. Holopeids are apparently mainly dextral but the Devonian *Antitrochus* is sinistral.

The strong flattened crescentic callus of *T. aerumnans* invites comparison with some genera of the family Anomphalidae but apertural characters are dissimilar. Moreover, the multispiral operculum of *Turbiniopsis* confirms its orthostrophic character (Tyler 1965).

A third possibility for comparison is found with members of the superfamily Euomphaloidea, traditionally regarded as gastropods but tentatively interpreted as paragastropods by Linsley and Kier (1984). The variability of shell morphology seen in *T. aerumnans* is also present in *Straparollus*, and the whorl profile in many euomphaloids is also a point of similarity. On the other hand, the multispiral operculum of omphalocirrids and the similar opercula of oriostomatids do not compare well with the paucispiral operculum of *T. aerumnans*. However, the great diversity of opercular form

PEEL AND HORNÝ: DEVONIAN GASTROPOD

within the trochacean gastropods recorded by Hickman and McLean (1990) casts doubt upon the utility of this character in gastropod classification.

Horný (1992) placed *Tychobrahea* within a new family, Tychobraheidae, together with *Komenskyspira* and *Asinomphalus*. Unfortunately, opercula are not known in these two genera. Other possible candidate family members include *Micromphalus*, *Straparollina* and some genera currently classified within the Anomphalidae, although opercula are not known in these taxa. It is likely that some species assigned in the literature to the genera *Straparollus* and *Holopea* are also tychobraheids.

Acknowledgements. A grant from the Swedish Natural Science Research Council (NFR) to JSP allowed RJH to bring *Tychobrahea aerumanns* to Uppsala for study.

REFERENCES

- BOUCOT, A. J., JOHNSON, J. G., HARPER, C. and WALMSLEY, V. G. 1966. Silurian brachiopods and gastropods of southern New Brunswick. *Bulletin of the Geological Survey of Canada*, **140**, 45 pp.
- COX, L. R. 1960. Gastropoda. General characteristics of Gastropoda. 184–1169. 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.
- FRETTER, V. and GRAHAM, A. 1994. *British prosobranch molluscs* (revised and updated edition). The Ray Society, London, 820 pp.
- GOULD, S. J. 1993. *Eight little piggies. Reflections in natural history*. Jonathan Cape, London, 479 pp.
- GUBANOV, G. P. and YOCHELSON, E. L. 1994. A Wenlockian (Silurian) gastropod shell and operculum from Siberia. *Journal of Paleontology*, **68**, 486–491.
- HICKMAN, C. S. and McLEAN, J. H. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Natural History Museum of Los Angeles County, Science Series*, **35**, 169 pp.
- HORNÝ, R. J. 1992. New Lower Devonian Gastropoda and Tergomya (Mollusca) of Bohemia. *Časopis Národního muzea, Řada přírodovědná*, **159**, 99–110.
- 1994. An isolated gastropod operculum from the Koněprusy Limestone, originally described as a shell of *Pleuronotus? confusus* Perner, 1903. *Časopis Národního muzea, Řada přírodovědná*, **161**, 83–84.
- KNIGHT, J. B. 1941. Paleozoic gastropod genotypes. *Special Paper of the Geological Society of America*, **32**, 510 pp.
- 1952. Primitive fossil gastropods and their bearing on gastropod evolution. *Smithsonian Miscellaneous Collections*, **117**, 1–56.
- COX, L. R., KEEN, A. M., BATTEN, R. L., YOCHELSON, E. L. and ROBERTSON, R. 1960. Systematic descriptions (Archaeogastropoda). 1169–1310. 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.
- LEVER, J. 1979. On torsion in gastropods. 5–23. In SPOEL, S. van der, BRUGGEN, A. C. van and LEVER, J. (ed.). *Pathways in malacology*. Scheltema and Holkema, Utrecht, 324 pp.
- LINDSTRÖM, G. 1884. On the Silurian Gastropoda and Pteropoda of Gotland. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **19**, 1–250.
- LINSLEY, R. M. 1978a. Shell form and the evolution of gastropods. *American Scientist*, **66**, 432–441.
- 1978b. Locomotion rates and shell form in the Gastropoda. *Malacologia*, **17**, 193–206.
- 1978c. The Omphalocirridae: a new family of Palaeozoic Gastropoda which exhibits sexual dimorphism. *Memoirs of the National Museum of Victoria*, **39**, 33–54.
- and KIER, W. 1984. The Paragastropoda: a proposal for a new class of Paleozoic Mollusca. *Malacologia*, **25**, 241–254.
- PEEL, J. S. 1984. Autecology of Silurian gastropods and monoplacophorans. *Special Papers in Palaeontology*, **32**, 165–182.
- 1987. Class Gastropoda. 304–329. In BOARDMAN, R. S., CHEETHAM, A. H. and ROWELL, A. J. *Fossil invertebrates*. Blackwell Scientific Publications, Oxford, 713 pp.
- 1992. The classes Tergomya and Helcionelloida, and early molluscan evolution. *Bulletin of Grönlands geologiske Undersøgelse*, **161**, 11–65.
- PERNER, J. 1903, 1907, 1911. Gastéropodes. In BARRANDE, J. *Système silurien du centre de la Bohême*. Musée Bohême, Prague, **4**(1), 164 pp.; **4**(2), 380 pp.; **4**(3), 390 pp.

- POJETA, J. and RUNNEGAR, B. 1976. The paleontology of rostroconch molluscs and the early history of the Phylum Mollusca. *US Geological Survey Professional Paper*, **968**, 88 pp.
- RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. *Journal of Paleontology*, **40**, 1178–1190.
- ROBERTSON, R. 1993. Snail handedness. *National Geographic Research & Exploration*, **9**, 104–119.
- ROHR, D. M. 1979. Geographic distribution of the Ordovician gastropod *Maclurites*. 45–52. In GRAY, J. and BOUCOT, A. J. (eds). *Historical biogeography, plate tectonics, and the changing environment*. Oregon State University Press, Corvallis, Oregon, 500 pp.
- and BOUCOT, A. J. 1985. Observations on the operculum of *Oriostoma* (Silurian Gastropoda). *Canadian Journal of Earth Sciences*, **22**, 294–296.
- TELLER, E. L. 1910. An operculated gastropod from the Niagara Formation of Wisconsin. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters*, **16**(2), 1286–1288.
- TRACEY, S., TODD, J. A. and ERWIN, D. H. 1993. Mollusca: Gastropoda. 131–167. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman and Hall, London, 845 pp.
- TYLER, J. H. 1965. Gastropods from the Middle Devonian Four Mile Dam Limestone (Hamilton) of Michigan. *Journal of Paleontology*, **39**, 341–349.
- VERMEIJ, G. J. 1975. Evolution and distribution of left-handed and planispiral coiling in snails. *Nature*, **254**, 419–420.
- 1993. *A natural history of shells*. Princeton University Press, Princeton, New Jersey, 207 pp.
- YOCHELSON, E. L. 1979. Gastropod opercula as objects for paleobiogeographic study. 37–43. In GRAY, J. and BOUCOT, A. J. (eds). *Historical biogeography, plate tectonics, and the changing environment*. Oregon State University Press, Corvallis, Oregon, 500 pp.
- 1990. Billings' second operculum: a late Early Ordovician *Maclurites* (Gastropoda) from western Newfoundland and the Canadian Arctic. *Canadian Journal of Earth Sciences*, **27**, 669–676.
- and LINSLEY, R. M. 1972. Opercula of gastropods from the Lilydale Limestone (Early Devonian) of Victoria, Australia. *Memoirs of the National Museum of Victoria*, **33**, 1–14.
- and WISE, O. A. 1972. A life association of shell and operculum in the Early Ordovician gastropod *Ceratopea unguis*. *Journal of Paleontology*, **46**, 681–684.

JOHN S. PEEL

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

RADVAN J. HORNÝ

Department of Palaeontology
National Museum
11579 Prague 1
Czech Republic

Typescript received 21 August 1995

Revised typescript received 20 November 1995