ANOMALOUS OCCURRENCES OF THE LOWER PALAEozoIC BRACHIOPOD SCHIZOCRANIA

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ABSTRACT. There are rare occurrences of Ordovician and Silurian species of the inarticulate brachiopod Schizocrania attached to orthoconic cephalopod shells. These were probably transported considerable distances prior to their deposition in onshore sediments, in which Schizocrania is not normally found. Relationships between host and encraster are discussed with a view to elucidating both encrustation sequences and inferred ecological associations.

DURING the course of studies of Upper Llanvirn, Ordovician (MGL) and Whitchiffan, Silurian (DDJA) successions in the Anglo-Welsh region, we noted rare occurrences of orthococones with Schizocrania (Trematidae) attached to either the inner or outer walls of their body chambers; in both cases the associated elastic sediments are of a coarse arenaceous type associated with demonstrably shallow-water facies (Williams 1953; Antia 1979). Havlíček (1972, p. 230) reported that the Upper Ordovician trematid Psychopetelis incola Perner from Bohemia: "...lived attached only to the cylindrical shells of orthococonid nautiloids;" he also noted that its ancestor P. hortui Havlíček sometimes encrusted orthococones. We therefore consider that these examples of apparent host-specific relationships may be paralleled elsewhere among the Trematidae (e.g. Schizocrania) by similar associations between host and encraster.

MATERIAL

The Upper Llanvirn specimen is an incomplete, poorly preserved internal mould of a body chamber of an orthococonid nautiloid of unknown taxonomic affinity. It was recovered from a shell-bed in the upper part of the Flags and Grits Formation exposed at Coed Dafon, 3 km south of Llangadog, Dyfed (Grid Ref. SN 792756), where it lay parallel to bedding. The orthococon has three specimens of Schizocrania cf. salopiensis Williams attached to the inner surface of the body chamber; the brachial valves all face inwards (text-fig. 1a) but show no obvious preference for any particular attachment site although two of the specimens are aligned subparallel to each other near the anterior end.

The Whitchiffan specimens are represented by poorly preserved fragmentary moulds of Orthiscarus sp. (diameters c. 20 mm and > 30 mm respectively) from the Lower Whitelee Beds of Mortimer Forest, south of Ludlow (Grid Ref. SO 477725) and the Upper Whitelee Beds near Broadstone Farm (SO 544000). The older specimen, an internal mould of a large portion of the conch (text-figs. 1a, 2a) has three specimens of S. striata (Sowerby) attached to the anterior part of its external surface. The specimens all occur close to each other on the exposed section of the orthococon mould which faces downwards from the undersurface of a bedded unit, relative to the final encondiment position of the orthococon; Schizocrania specimens occur on its 'underside' and following the dissolution of the cephalopod shell have become impressed on to the preserved mould. The younger (upera Whitchiffan) specimen consists of the internal and external moulds of a curved fragment of a large body chamber; it has five poorly preserved specimens of S. striata attached to its inner (concave) surface which faces downwards. The specimens are aligned transversely, parallel to the peristome (text-figs. 1, 2c).

The lectotype (Geol. Surv. Mus. No. 6631) of S. striata (Sowerby) from the Leintwardine-Whitchiffan beds of Delbury, Salop (Grid Ref. SO 501845) is the only other known British Schizocrania which we have discovered attached to an orthococon nautiloid fragment; the specimen is attached to the convex surface of the free part of a septum, probably the last one; it differs from the other examples in its larger size (length 9 mm) and posterior attachment site (text-fig. 2a).
OBSERVATIONS AND INTERPRETATION

All twelve of these *Schizoceratium* specimens exhibit only their convex brachial valves facing away from the cephalopod shell surface. *Schizoceratium* is known to attach to substrates by its flat pedicle valve (Hall and Whitfield 1875; Rowell in Williams *et al.* 1965, p. H283). However, pedicle valves are exceptionally rare, being either altogether absent from assemblages or hidden from view beneath the brachial valve. The three orthocone specimens shown in text-fig. 1 indicate that the anterior edge of the phragmacone was the preferred encrustation site for all but two of the *Schizoceratium* specimens. The orientation of these *Schizoceratium* inside the phragmacone and on the shell exterior is apparently not random since all adjacent shells are aligned with their umbones pointing in approximately the same direction (i.e. transverse or oblique to the orthocones’ long axis).
The orthocones may have been encrusted while they were alive and mobile, or when they were dead and floating, or dead and semi-buoyant, being washed around on the sea floor, or dead and settled on the sea floor, or, finally, when being reworked.

In addition to the numerous examples of fossil cephalopod (ammonoid) encrustation recorded from Mesozoic assemblages (e.g. Seilacher 1960; Meischner 1968) and the few broadly analogous Lower Palaeozoic examples involving orthoconic nautiloids (Holland 1971; Hav-Rock 1972), we have noted Ordovician and Silurian collections containing several varied and undescribed examples of orthocone encrustation (e.g. National Museum of Wales specimen NMW 79, 5G, Map loc. 771; Hunterian Museum specimens S.25129/1-3 and S.25114 a/b). *Schizocrania* is ornamented by numerous radial capillae (Williams 1974, p. 44). According to Williams and Wright 1963, p. 19 and Williams and Rowell (in Williams et al. 1965, p. H81) such radial ornament probably supported setal follicles at the commissure, and it is reasonable to assume that *Schizocrania* was particularly setiferous. Sudarson (1969, p. 65) noted that *Discinisca* larvae have well-developed principle setae and that 'there may be a prolonged larval stage... with chaetae increasing in number to facilitate flotation'. Both the *Schizocrania* species discussed here exhibit high capillae densities at the same

TEXT-FIG. 2. a. *Schizocrania striata* lectotype showing attachment to mould of orthocone septum from upper Ludlow beds, Delbury, Shrops., x 3. a. Detail of *S. striata* specimens BP94078 (left) and BP94079 (right) from Lower Whitcliffe Beds, Mortimer Forest, Ludlow, x 12.5; see also text-fig. 1a. c. *S. striata* specimens BP94081 (top) to BP94085 showing attachment to orthocone body chamber fragment, the edge of which is arrowed, from Upper Whitcliffe Beds, Broadstone Farm, Ludlow, x 6. Text-fig. 1c is a scale-drawing of the counterpart of this specimen.
growth stage (i.e. 10–12 per mm, 5 mm antero-medianly of the dorsal umbones) and probably therefore had a juvenile epipelic stage.

Holland (1971, p. 18) considered that strophomenid (aegeromenid) and rhychnellid (Microsphaeridorynchus mcullai) brachiopods might have attached to living orthoconic hosts but concluded that due to the size of the brachiopods this was 'unlikely'. Havišček (1967, p. 21) demonstrated the attachment of epipelic strophomenids to the 'stems of algae' (Havišček 1967, p. 21). He subsequently suggested (Havišček 1972, p. 230) that aegeromenids attached to living orthocones and considered that inarticulates such as Psychopolites incola 'were attached to the shells of living nautiloids' (Havišček 1972, p. 230) whilst related trematids attached both to orthocones and other specific 'freely moving organisms' (Havišček 1972, p. 229). An orthocone encrusted with Conchulites (Ordovician) was described by Prantl (1948, p. 6). Sellacher (1954, 1968) concluded (1968, p. 284) that the preferentially orientated epizoans on this specimen were adjusted to the 'head-on motion of their host'. Both Havišček (1972, p. 230) and Sellacher (1968) suggested that preferred orientation of encrusters is of prime importance in testifying to pre-mortem attachment. This suggests that the majority of known Schizocerania specimens were attached at various stages in the orthocone's post-mortem history. Although Havišček (1972, p. 229) presumed that aegeromenid brachiopods such as those depicted by Holland (1971, fig. 1b) attached to live orthocones, direct evidence for this is insubstantial. Although these authors, and Bergström (1968) have shown such brachiopods attached in rows along orthocones and 'algal stems' such arrangements do not constitute the type of preferred orientation referred to above.

Since modern spirobids are known to be host specific and capable of seeking a preferred attachment site and orientation (Knight-Jones 1951), it is almost certain that the occurrence of fossil spirobids aligned along the growth margins of orthocones (Holland 1971) indicates a comparable relationship. This may mean that the similar alignment of Schizocerania specimens noted here (text-fig. 1) could also be indicative of a host-specific relationship. Such a contention tends to be supported by our observation that the Anglo-Welsh Schizocerania have not been found attached to any other host organisms and would also offer a possible explanation for the virtual absence of pedicle valves, which could have either remained attached to a host when the brachial valve disarticulated, or become obscured during fossilization by the substrate to which they were attached.

The Schizocerania on the internal surface of the body chambers of the Llanvirn and upper Whitcliffian specimens indicate encrustation beginning no earlier than the post-mortem drifting phase (following decay of mantle lining the body chamber) but prior to the infilling of the body chamber. Interpretation of the lower Whitcliffian orthocones' pre-entombment history is problematic; it could have been encrusted at any one of a number of stages in its history as a live or dead mobile organism. However, since the Schizocerania are attached to its 'underside' they must have settled and had time to grow prior to its final entombment in this position. The S. straita lectotype must have become attached to the posterior side of its septal substrate after the separation of the orthocone's body chamber from the remaining posterior part of the shell (i.e. at a relatively late stage in the orthocones' post-mortem history).

On the lower Whitcliffian orthocone the internal mould (text-fig. 1b) is covered by numerous irregular markings consisting mainly of small elongated raised protruberances averaging about 0-1 mm in height and width and between 0-3 and 0-7 mm in length. These apparently represent the internal moulds of bryozoan borings on the inner surface of the orthocone shell although it is not altogether clear whether some of the flatter or even slightly indented markings may not result from the fossilization of external borings. In any event where the Schizocerania shells are slightly broken, and around their edges, it is evident that the borings affect the orthocone shell beneath. Unfortunately the absence of a counterpart of this specimen renders this evidence inconclusive.

**Distribution of Schizocerania**

The Llanvirn orthocone and Schizocerania discussed here are virtually the only representatives of these taxa known from the predominantly arenaceous and rudaceous Fairflach Group of the Llandeilo area. Since S. salopiensis is common in penecontemporaneous, argillaceous successions
elsewhere in South Wales and the Welsh Borderlands (Williams 1974; Bassett et al. 1974. p. 9; Lockley and Williams, in press) where there are different benthic and pelagic faunas (i.e. trilobites, graptolites, and cephalopods), it is reasonable to assume that the exotic Fairfach occurrence may have been related to the drifting or migration of a stray cephalopod beyond the normal limits of its indigenous environment. Such post-mortem drifting of modern cephalopods is well known (House 1973; Kennedy and Cobban 1976; Hewitt and Pedley 1978) and may result in individual specimens being transported for hundreds or even thousands of kilometres.

Similarly S. striata is rare in the Whitecliff Beds of the Ludlow region where it constitutes only about 0-01 to 0-005% of the total fauna with specimens generally occurring in a fragmentary condition and random orientations. It is more common in unbioturbated, parallel-laminated, alternating light and dark silstones (rhythmites) of deeper-water facies (e.g. Upper and Lower Leintwardinian Beds, Holland et al. 1963, p. 154; Lawson 1973, p. 274) and is recorded only rarely in shallow-water bioturbated silstones (Facies B sensu Antia 1979). Again, the Whitecliffian cephalopods drifted into inshore deposits from an offshore source, although limited evidence also points to later phases of encrustation (e.g. lectotype). Williams (1969, p. 143) discussed the potential range of larval dispersal and its bearing on brachiopod migration during the Ordovician. Clearly his suggested figure (up to 250 km) is only a fraction of the range potential for brachiopods capable of encrusting live or drifting orthoclines.

Trematid hosts

Encrusting Trematidae such as Schizocrania, Drahodiscina, and Ptychopelitis appear to have been host specific. S. salopiensis, S. striata, and P. palaea have hitherto only been observed attached to orthoconic nautiloids generally presumed to have been alive or floating at the time of their encrustation. Other members of the family, e.g. P. hornyi Haviček and D. grandis Barrande, are commonly attached to conularis which are considered by Haviček (1972) to have been mobile during life, and the American species S. filosa Hall frequently attached to the brachiopod Rafinesquina (e.g. Cooper 1956 and Rowell in Williams et al. 1965). With respect to trematid-nautiloid associations, it is intriguing to note that Titus and Cameron (1976) record S. filosa only in their deep-water Geisonoceras (Orthocerida) community. Dr. R. A. Hewitt and Mrs. D. Evans (pers. comm. 1979) inform us that they know of no Silurian or Ordovician examples of cephalopod encrustation by brachiopods other than those reported here, which is suggestive of host-specific relationships.

CONCLUSIONS

Faunal associations with abundant Schizocrania in the Ordovician and Silurian of the Anglo-Welsh region are almost invariably confined to argilloaceous deep-water facies where species of the genus are represented almost exclusively by assemblages of brachial valves. Such exceptionally disproportionate valve ratios are considered to result from their encrusting habits which might account for the obscuring or removal of pedicle valves. Known associations between trematid encurers and hosts such as those reported here and elsewhere (e.g. Haviček 1972; Rowell in Williams et al. 1965) point to some form of host-specific relationship between representatives of the family and other larger invertebrate hosts. Whether such relationships could be termed symbiotic, commensal, or parasitic is unclear because we lack evidence which demonstrates that hosts were encrusted during life. However, we can establish that encrustation of orthoclines, which may in some cases have begun during their life, often began no earlier than the post-mortem drifting phase, and may have continued or begun at a time when the orthoclines were resting or rolling on the sea floor. Since encrustation of many of these orthoclines could not have taken place when they were in the final 'resting' position it must have occurred during the middle phases of their pre-entombment history.

The following suggestions on the time of encrustation can be made: (1) The encrusting Schizocrania noted here are not currently known to attach to non-orthocone skeletal components within the deposits from which they were recovered and are therefore likely to have settled
preferentially on orthocoene shells prior to their final deposition. (2) The apparent high-density, orderly clustering of Schizocorania towards the anterior of the conch suggests that possibly the orthocoene was colonized as a specific host whilst it was floating. (3) Since both Schizocorania and its nautilloid hosts are normally indigenous to sparsely fossiliferous, low-density offshore facies, it is probable that encrustation occurred in an offshore region before the orthocoenes finally became entombed in more diverse, fossiliferous, onshore facies where Schizocorania is invariably rare. This inference is supported by the observation that the setiferous Schizocorania may well have been adapted to a prolonged larval stage which would have enhanced its chances of encountering a suitable encrustation site. If Schizocorania even occasionally encrusted orthocoenes in a manner analogous to the attachment of epiplanctic aenigmata to buoyant organisms noted by Bergström (1968), then the combined effect of nautilloid mobility during life and drifting after death would offer an explanation for exceptionally widespread occurrences of certain kinds of brachiopods.

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