SEDIMENT "WHIPS": AMPHIPOD ARTEFACTS FROM THE ROCKY SUBLITTORAL IN BRITAIN

P. G. Moore

University Marine Biological Station, Millport, Isle of Cumbrae, KA28 0EG, Scotland

and

R. Earll

Marine Conservation Society, 4 Gloucester Road, Ross-on-Wye HR9 5BU, U.K.

(Received 5 March 1985; revision received 19 April 1985; accepted 25 April 1985)

Abstract: Sediment whips are reported attached to hydroids from circalittoral boulder grounds off St. Abbs, Scotland which are thought to be artefacts constructed by the amphipod Dyopedos porrectus Bate. Whips have been photographed in situ supporting primarily Dyopedos, but additionally caprellid amphipods and the arcturid isopod Astacilla longicornis (Sowerby). Under the scanning electron microscope the surface of the whip is seen to be criss-crossed with a meshwork of microfibrils thought to be derived from dactylar secretions of peraeopods 3 and 4 of Dyopedos. These impart significant strength and flexibility to whips underwater. The function of a whip is thought to be that of a vantage point for suspension-feeding.

Key words: Dyopedos; sediment whips; Amphipoda; hydroid mimicry; Scotland

INTRODUCTION

The common occurrence of “whips” (Figs. 1, 2) attached to the hydroids Tubularia spp. (predominantly), Thuja thuja (L.) and Abietinaria filicula (Ellis & Solander) on circalittoral boulder grounds at depths > 20 m all along the exposed rocky coastline near St. Abbs, Berwickshire (55°52.0′: 2°4.0′) has been known to us for some time, but their provenance and function remained an enigma until now.

METHODS

Samples were taken by SCUBA diving using standard techniques. Individual whips were collected into small tubes stoppered in situ and subsequently preserved in 70% ethanol. Material for scanning electron microscopy was air-dried. Segments of whip were mounted on stubs using double-sided tape and examined in a Philips SEM-500 instrument.
RESULTS AND DISCUSSION

Typically, whips are $5.2 \pm 0.2$ (SD) cm in length ($n = 3$). They are usually widest at the point of attachment ($\approx 500 \mu m$) and taper, more or less, to a blunt point distally. At first they were dismissed as decaying hydroid stems but closer inspection revealed that they were composed of sediment and that all (of several dozen examined in situ in August 1984) supported a number of epifaunal peracarid crustaceans. The clear implication was that these structures were elaborated by one or more of these organisms.

Recently, one of us (R.E.) has photographed these sediment whips plus their associates underwater (Fig. 1A–C) and it is clear from the photographs and from

Fig. 1. Sediment "whips" photographed in situ off St. Abbs, Berwickshire: A, two whips constructed on Abietinaria, the longer supporting Dyopedos distally and Astacilla proximally — note the resemblance to a hydroid; B, unidentified caprellid amphipod utilizing Dyopedos whip; C, two large and six small Dyopedos (?male/female/juveniles) on whip.
voucher material examined by P. G. M. that several peracarid species utilize the whips, viz. the arcturid isopod *Astitella longicornis* (Sowerby), a caprellid amphipod (as yet uncaptured), and, most commonly, the podocerid amphipod *Dyopedos porrectus* Bate. Each of these types is morphologically adapted for clinging and climbing (see Wetzel (1932) on caprellids; Enequist (1949) and Laubitz (1979) on podocerids; Moore (1985) on arcturids) and it is likely that the whips are constructed to serve as vantage points for suspension-feeding.

The question as to the manner of whip construction remains open: no building behaviour having been observed in situ. Circumstantial evidence, however, strongly implicates *Dyopedos* as the organism responsible. It is the commonest species in preserved samples and no records exist of the other peracarids (or related species) indulging in such constructional activities. For podocerid amphipods, on the other hand, there do exist observations made by McCloskey (1970) of similar detrital rods being manufactured by *Dulichia rhabdothelis* and cemented to the tips of sea urchin spines, and Laubitz (1979) included mention of unpublished work off Labrador which linked *Dyopedos porrectus* with rod-building there. McCloskey’s account of the discovery of these structures prescribed our experience in that they were known to divers but initially held to be merely streamers of decaying debris. McCloskey (1970) stated that rods were built up by *Dulichia* using its faeces cemented together with oral secretions, and that, during the summer, *D. rhahdoplastis* actively “gardened” diatoms growing on the rods — weeding and cropping them as micro-pastures — a behaviour which he suggested was without parallel in any other marine crustacean. In winter, *D. rhahdoplastis* used the bare rods as vantage points for suspension feeding.

Scanning electron microscopy of a whip collected in August 1983 revealed interesting details of construction (Fig. 2) but no major diatom epiphras was observed (a few coccoliths (?) diatoms and the odd foraminiferan and dinoflagellate were present on the whip scanned). The whip appeared to be built up as a wound spiral (cf. a “Swiss roll”) with a longitudinal edge apparent over much of its length. The external surface of the structure (Fig. 2) was covered in a fine meshwork of micro-fibrils (≈0.2–0.3 μm diameter), presumed to be stretched silk secretions emanating from the dactyli of the amphipods’ anterior peraeopoda. Appropriately the terminal pore of P3 dactylus of a mature male *Dyopedos* measured ≈1 μm diameter. The resultant meshwork is reminiscent of geodetic construction of aircraft fuselages and would confer relative strength together with flexibility. Whips are brittle when dry, but when wet they can be twisted and bent to a quite remarkable extent.

The word “whip” is preferable to “rod” for these structures attributed to *Dyopedos porrectus* (see also Laubitz, 1979); they are substantially longer than those described for *Dulichia rhabdothelis* by McCloskey (1970) and are also markedly flexible.

While undisturbed, *D. porrectus* “line-up”, heads distally, along the whips. The maximum number of organisms counted to date on a single whip is 15 *Dyopedos* + 1 *Astitella*, see Fig. 1A. (It is interesting that in Figs. 1A and B both *Astitella* and the caprellid face proximally.) When the whip is prodded gently, the *Dyopedos* shuffle
Fig. 2. Scanning electron microscope photographs of surface of whip (transverse view) at successively higher magnifications: whip collected off St. Abbs in August 1983 attached to hydroid *Thuaria thuya*; note longitudinal ridge (l.r.) and meshwork of fine micro-fibrils (m.f.).
backwards proximally down the whip in an orderly, reversing queue. It is tempting to speculate that the *Dyopedos* shown in Fig. 1C (2 adults + 6 juveniles) may represent a family group (cf. Laubitz, 1979 below).

Prior to McCloskey’s (1970) exciting revelations about *Dulichia rhabdoplastic*, data on the biology of podocerid amphipods were limited to the aquarium observations of Enequist (1949). Laubitz (1979), however, reported unpublished observations made by R. Hooper on rod-building by “several” species off the Atlantic and Pacific coasts of Canada. Hooper observed *Dyopedos porrectus* off Labrador, where they build whips up to 100 mm long of detritus, faeces and mucus. They were usually built on other organisms, in one case on the top of colonies of the hydroid *Lafoena maxima* and each was occupied by one or two adults, and young of up to 3 months.

Our observations support and extend these reports for *Dyopedos porrectus*, further strengthening the possibility that this constructional activity might be of widescale occurrence in this highly derivative gammaridean family (as speculated initially by McCloskey). Such a biology would help to explain their infrequent capture using remote gear. Their small size, their association with hard ground, the relative fragility of their artefacts, together with the amphipods’ considerable swimming ability (Enequist, 1949; McCloskey, 1970) would all mitigate against their regular encounter by any means other than by diving. The paucity of records of *D. porrectus* in British regional amphipod faunas (Jones, 1948; Hamond, 1967; Moore, 1984) is thus more likely to be the result of the summation of these tendencies, rather than the consequence of genuine rarity.

The distinct absence of whips from the immediate sublittoral fringe and infralittoral zone off St. Abbs is doubtless due to the incompatibility of such fragile structures (even granted their structure) with the severe surface-water wave action experienced along this exposed coastline. Geographically, *D. porrectus* ranges across the north Atlantic from Novaya Zemlya and western Greenland southwards to northwestern France and Cape Cod (Laubitz, 1977). It is usually associated with hydroids and bryozoans (Lincoln, 1979).

The brownish/maroon body pigmentation of *D. porrectus* is narrowly banded transversely according to Sars (1890). Although narrow transverse pigment bands are present dorsally along segmented junctions of the peraeon, in the largest female presently available, most pigment is concentrated longitudinally along the ventral surface in the mouthpart bundle, limbs, pleopods, ventrally-curled urosome and oostegites – a pattern which would certainly contribute to crypsis in the dimly-lit circalittoral – especially when viewed against a linear habitat. This would help to compensate for a life-style so apparently vulnerable to fish predation (see also McCloskey, 1970), but perhaps a whip loaded with *Dyopedos, Astacilla* and caprellids (cf. stick insects) reasonably mimics a hydroid stalk (see Fig. 1A)? After all, other amphipods mimic gastropods (Crane, 1969) and shrimp eggs (Bowman & Wasmer, 1984).

Detailed work on the in situ behaviour of these little-known and inaccessible amphipods will not be easy to accomplish, but it would throw fascinating light on the
phylogenetic constructs of systematists concerning the evolutionary derivation of caprellids from an ancestral gammaridean amphipod stock (vide Laubitz, 1979). Virtually nothing has been published on the architecture of amphipod artefacts constructed by the domicolous families. Meadows et al. (in press) report the fine structure of the silk lining of the burrows of Corophium volutator. Great scope would seem to exist for studies of the ecological and phylogenetic significance of different "knitting patterns".

On the basis of evidence presented here it is much more likely (see also Shillaker & Moore, 1978) that peraeopodal, rather than mouthpart, secretions are involved in mesh production by Dyopedos (cf. McCloskey, 1970). Laubitz (1977) was uncertain as to the glandular nature of podocerid P3 and 4 but pointed out that the inflated limb bases have a glandular appearance in external view. Our findings support the contention that Dyopedos peraeopods are glandular; indeed the dactylus is also swollen sub-terminally in our specimen and appears itself to contain secretory tissue.

ACKNOWLEDGEMENTS

We would like to thank Mr. L. Tetley and Mrs. H. Hendry (Glasgow University Zoology Department) for technical assistance with the scanning electron microscope and Dr. C. Edwards (S.M.B.A., Oban) for identification of Abietinaria filicina.

REFERENCES


