ATTACHMENT TO GASTROPOD VELIGER SHELLS - A POSSIBLE MECHANISM OF DISPERSAL IN BENTHIC FORAMINIFERANS

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ABSTRACT
A benthic, calcareous foraminiferan cf. *Pararotalia venusta* (Brady, 1884) was in five cases found attached to the shell of the veliger larva of the muricid gastropod *Thais javanica* (Philippi, 1846). Observations showed that such foraminiferans are able to move onto and attach to the larval shell and that the swimming veliger larva is able to carry this load. Most other dispersal mechanisms described in foraminiferans occur in shallow water or are of local importance. In contrast to them, this mechanism may be important for long-distance dispersal also over the sublittoral or in the deep-sea and even between separated deep-sea areas.

INTRODUCTION
Few studies of dispersal in foraminiferans have been made (Bock 1970; Buzas *et al.* 1977; Bernstein *et al.* 1978; Lessard 1980; Spindler 1980; Lipps 1982; Hayward 1983; Palmer & Gust 1985; Buzas & Culver 1989, 1991; Benzie 1991) and most of the existing knowledge is based on occasional observations (Gerlach 1977). Also, very little is known about the dispersal mechanisms. One of these is epizoic dispersal. Foraminiferans have been found attached to a variety of motile organisms (Rieth 1957; Zann *et al.* 1975; Farmer 1977; Mullineaux & DeLaca 1984; Moore 1985; Cedhagen 1988; Rosso & Sanfilippo 1991; Brown & Berkman 1992; De Vantier 1992; Plaziat 1993; Svavarsson & Davidsdottir 1995). Most of these organisms live in fairly shallow water or do not cover long distances.

There is some evidence as to the capability of foraminiferans to disperse effectively: (1) Foraminiferans are very common fossils since the Palaeozoic Era and have been used as stratigraphic „markers", because many of them have a wide geographic distribution and a short geologic occurrence (*eg* Buzas & Culver 1989, 1991). (2) Some foraminiferans are obligate parasites which are common on hosts with a scattered distribution, *eg* sessile bivalves (Cedhagen 1994), or live as hyperparasites on parasitic gastropods living on deep-sea crinoids (Warén & Carney 1981). (3) Genetic distances between foraminiferans in the western Coral Sea, and on the Great Barrier Reef suggest the presence of long-distance dispersal (Benzie 1991). (4) Foraminiferans have also been recorded in colonisation experiments (*eg* Wefer & Richter 1976; Widbom 1983; Cedhagen unpubl.). These studies and observations suggest that foraminiferans disperse effectively.

The present observations may fill a gap in the knowledge of long-distance dispersal.

MATERIAL AND METHODS
Egg capsules and larvae of the muricid gastropod *Thais javanica* were reared in aquarium at the Phuket Marine Biological Centre, Thailand, as described by Middelfart (1998). About 300 competent larvae of *T. javanica* were collected and examined after 20 days of pelagic development.

RESULTS
Five of the 300 larvae carried each a single foraminiferan, *viz Pararotalia* cf. *venusta* (Brady, 1884), attached to the shell (Fig. 1).

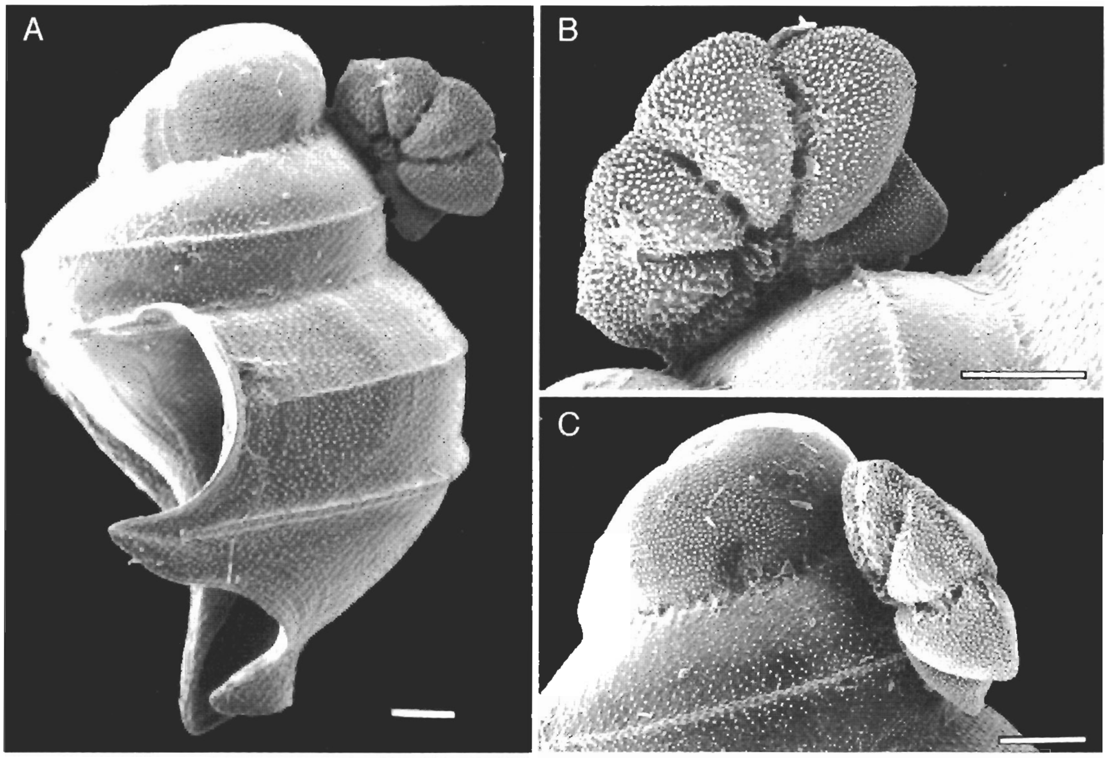

Figure 1. A-C. The veliger shell of the muricid gastropod *Thais javanica* with the foraminiferan *Pararotalia* cf. *venusta* attached to it. The scale bar indicates 100 µm.

All of the foraminiferans were located on the same part of the shell, *viz* on that side of it that is directed downwards when the larva swims (Fig. 2).

DISCUSSION

Although the observations were made in aquarium, they show that the foraminiferans are able to move onto the veliger shell and attach to it and that the veliger larvae are capable of carrying these epibionts when swimming.

The size of the foraminiferan shows that the foraminiferan is probably older than the gastropod larva (Boltovskoy & Wright 1976). Consequently, the foraminiferan has actively moved onto the gastropod after living elsewhere previously. This agrees with the fact that the genus *Pararotalia* has been reported to contain free-living herbivorous species that live clinging to substrata in inner shelf environments (Murray 1991).

As mentioned above, the foraminiferans were in all cases attached to the same part of the veliger shell, *viz* that side which is directed downwards when the larvae swim. Two explanations for this are possible: (1) The velum or other soft organs of the larva remove epibionts within their reach, so that the position of the foraminiferans must be outside of that reach. However, we have neither any observations nor any literature information to support this hypothesis. (2) The second explanation is that the foraminiferan moves onto the shell when the veliger larva is close to the bottom. We find this explanation more plausible, as the foraminiferans are attached to that part of the shell that most likely will come into contact with the bottom.

There are a few parallels to our observations. Some veliger larvae are capable of long

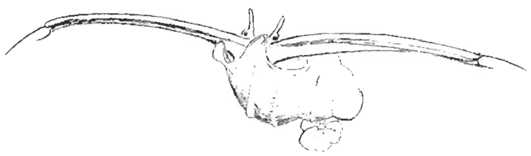

Figure 2. Diagrammatic drawing showing the orientation of the swimming veliger larva of *Thais javanica* and the position of the epibiotic foraminiferan (F).

distance dispersal and can carry other organisms. Scheltema (1973a,b) found that the sessile ciliate *Folliculina simplex* maintains its wide distribution, across the entire Atlantic Ocean, through epizoic dispersal by gastropod veligers with a prolonged larval period, so-called teleplanic larvae. Our observations show that this method may be used by benthic foraminiferans as well. Dr Kurt W. Ockelmann (pers. com.) has observed several cases of foraminiferans attached to the shells of juvenile bivalves drifting with the help of a byssus thread.

Benthic foraminiferans are often found on the hulls of ships and on drifting objects like wood, algae, coconuts, and seaweed (*eg* Gerlach 1977). This type of dispersal is possible only for foraminiferans living in eulittoral or shallow sublittoral environments. This is also true for the cases mentioned in the Introduction. Most of the organisms reported to carry foraminiferans over the sublittoral or in the deep-sea do not cover long distances. Some deep-sea molluscs have planktotrophic veliger larvae (Bouchet & Warén 1979) that migrate to the sea surface during their development (Bouchet & Fontes 1981; Bouchet & Warén 1994). Dispersal with the help of such larvae may be an important mechanism of long-distance dispersal over the sublittoral or in the deep-sea and even between deep oceanic areas separated by shallow areas.

Further observations are needed. It is important to find out whether the mechanisms discussed is a common phenomenon or not and examination of plankton samples from the open sea could be one way to achieve this.

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REFERENCES

Benzie, J.A.H. 1991. Genetic relatedness of foraminiferan (*Marginopora vertebralis*) populations from reefs in the western Coral Sea and Great Barrier Reef (Australia). - Coral Reefs **10**(1): 29-36.

Bernstein, B.B., R.R. Hessler, R. Smith & P.A. Jumars. 1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. - Limnology and Oceanography **23**(3): 401-416.

Bock, W.D. 1970. *Thalassia testudinum*, a habitat and means of dispersal for shallow water benthic foraminifera. - Transactions of the Gulf-Coast Association of Geological Societies **19**: 337-340.

Boltovskoy, E. & R. Wright. 1976. Recent foraminifera. Dr. W. Junk b.v. Publishers, The Hague, 515 pp.

Bouchet, P. & J.C. Fontes. 1981. Migrations verticale des larves de Gastéropodes abyssaux: arguments noveaux dûs à l'analyse isotopique de la coquille larvaire et post-larvaire. - Comptes Rendus de l'Academie des Sciences. Serie III, Sciences de la Vie (Paris) **292**(17): 1005-1008.

Bouchet, P. & A. Warén. 1979. Planktotrophic larval development in deep-water gastropods. - Sarsia **64**(1-2): 37-40.

Bouchet, P. & A. Warén. 1994. Ontogenetic Migration and Dispersal of Deep-Sea Gastropod Larvae. - Pages 98-117 *in*: Young, C.M. & K.J. Eckelbarger (eds.). Reproduction, larval biology, and recruitment of the deep-sea benthos. Columbia University Press, New York.

Browne, D.W. & P.A. Berkman. 1992. Epizooic foraminifera, tanaid, and polychaete species associations on Antarctic scallop shells. - Antarctic Journal of the United States **27**(5): 134-135.

Buzas, M.A. & S.J. Culver. 1989. Biogeographic and evolutionary patterns of continental margin benthic foraminifera. - Paleobiology **15**(1): 11-19.

Buzas, M.A. & S.J. Culver. 1991. Species diversity and dispersal of benthic Foraminifera. - Bioscience **41**(7): 483-489.

Buzas, M.A., R.K. Smith & K.A. Beem. 1977. Ecology and Systematics of Foraminifera in Two *Thalassia* Habitats, Jamaica, West Indies. - Smithsonian Contribution to Paleobiology: i-iii + 1-139.

Cedhagen, T. 1988. *Phoxichilidium tubulariae*, en dåligt känd svensk havsspindel. - Göteborgs Naturhistoriska Musei Årstryck: 35-37.

Cedhagen, T. 1994. Taxonomy and biology of *Hyrrokkin sarcophaga* n. gen. et sp. n., a parasitic foraminiferan (Rosalinidae). - Sarsia **79**: 65-82.

DeVantier, L.M. 1992. Rafting of tropical marine organisms on buoyant coralla. - Marine Ecology Progress Series **86**(3): 301-302.

Farmer, A.S.D. 1977. Epizoic foraminifera on *Nephrops norvegicus*. - Journal of the Marine Biological Association of the United Kingdom **57**: 877-878.

Gerlach, S.A. 1977. Means of Meiofauna Dispersal. - Mikrofauna der Meeresboden **61**: 89-103.

Hayward, B.W. 1983. Biogeography and dispersal mechanisms of benthic Foraminifera. - New Zealand Marine Sciences Society Newsletter **28**.

Lessard, R.H. 1980. Distribution patterns of intertidal and shallow-water Foraminifera of the tropical Pacific Ocean. - Cushman Foundation For Foraminiferal Research Special Publication **40**: 40-58.

Lipps, J.H. 1982. Biology/paleobiology of Foraminifera. - University of Tennessee Department of Geological Sciences Studies in Geology 1982 **1**: 1-21.

Middelfart, P. 1998. Egg capsules and larval development of some Muricidae (Gastropoda: Prosobranchia) from the Indo-West Pacific. - Ophelia, in press.

Moore, P.G. 1985. *Cibicides lobatulus* epizoic on *Astacilla longicornis* in the North Sea. - Journal of Natural History **19**: 129-133.

Mullineaux, L.S. & T.E. DeLaca. 1984. Distribution of Antarctic Benthic Foraminifers Settling on the Pecten *Adamussium colbecki*. - Polar Biology **3**: 185-189.

Murray, J.W. 1991. Ecology and Palaeoecology of Benthic Foraminifera. Longman Scientific & Technical, Essex, x + 397 pp.

Palmer, M.A. & G. Gust. 1985. Dispersal of meiofauna in a turbulent tidal creek. - Journal of Marine Research **43**(1): 179-210.

Plaziat, J.C. 1993. Modern and fossil potamids (Gastropoda) in saline lakes. - Journal of Paleolimnology **8**(2): 163-169.

Rieth, A. 1957. Vorkommen einer Foraminifere im Arterner Salzgebiet. - Mikrokosmos **47**: 100-105.

Rosso, A. & R. Sanfilippo. 1991. Epibionts distribution pattern of *Chlamys patagonia* (King & Broderip) of the Magellan Strait. - Memorie Di Biologia Marina E Di Oceanografia 1991 (1992): 237-240.

Scheltema, R.S. 1973. Dispersal of the Protozoan *Folliculina simplex* Dons (Ciliophora, Heterotricha) throughout the North Atlantic Ocean on the Shells of Gastropod Veliger Larvae. - Journal of Marine Research **31**(1): 11-20.

Scheltema, R.S. 1973. On an unusual means by which the sessile marine ciliate *Folliculina simplex* maintains its widespread geographical distribution. - Netherlands Journal of Sea Research **7**: 122-125.

Spindler, M. 1980. The pelagic gulfweed *Sargassum natans* as a habitat for the benthic Foraminifera *Planorbulina acervalis* and *Rosalina globularis*. - Neues Jahrbuch für Geologie und Palaeontologie Monatshefte (**1980**)9: 569-580.

Svavarsson, J. & B. Davidsdottir. 1995. *Cibicides* spp. (Protozoa, Foraminifera) as epizoites on the Arctic antenna-brooding *Arcturus baffini* (Crustacea, Isopoda, Valvifera). - *Polar Biology* **15**(8): 569-574.

Warén, A. & R. Carney. 1981. *Ophiolamia armi-*

geri gen. et sp. n. (Mollusca, Prosobranchia) parasitic on the abyssal Ophiuroid *Ophiomusium armigerum*. - Sarsia **66**: 183-193.

Wefer, G. & W. Richter. 1976. Colonization of artificial substrates by Foraminifera. - Kieler Meeresforschungen Sonderheft pp. 72-75 + 2 pls.

Widbom, B. 1983. Colonization of azoic sediment by sublittoral meiofauna in Gullmar Fjord, Swedish west coast. - Oceanologica Acta 1983. Proceedings 17th European Marine Biology Symposium, Brest, France, 27 September-1 October, 1982: 213-217.

Zann, L.P., R.J. Cuffey & C. Kropach. 1975. Fouling Organisms and Parasites Associated with the Skin of Sea Snakes. Pages 251-265 *in*: Dunson, W.A. (ed.). Biology of Sea Snakes. University Park Press, Baltimore, Maryland.

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