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A review of Recent and fossil serpulid 'reefs'; actuopalaeontology and the 'Upper Malm' serpulid limestones in NW Germany

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Abstract

Serpulidae (Polychaeta) are benthic, suspension-feeding worms, mostly marine, secreting their own calcareous habitation tubes. Serpulid 'reefs' include banks deposited on shallow parts of continental shelves, and primary frame reefs at intertidal and subtidal depths. Sheltered bays harbour the largest reefs, up to a few metres in height and kilometres in length. A review of habitats with Recent serpulid mass-occurrences allows interpretation of the palaeoenvironment in which the serpulid limestones in the 'Upper Malm' (Upper Jurassic-Lower Cretaceous) of NW Germany may have been laid down. The Lower Serpulid Limestones represent concentrations of re-deposited serpulid tubes. In the Upper Serpulid Limestones ('Serpulit') the re-deposited tubes are embedded in stromatolitic algae. Both limestones were formed in lagoons fringing an inland sea.

Several records of Recent and fossil 'serpulid' buildups are erroneous and can be referred to algae, vermiform 'gastropods' or non-serpulid polychaetes. Differences and similarities between calcareous tubes of serpulids and vermetids (Gastropoda) are summarized.

1. Introduction

1.1. Serpulids as sediment-source

Serpulids (Annelida, Polychaeta) are worms that build a calcareous habitation tube, which generally is attached to a submerged surface. On the whole, they do not constitute a major sediment source. In the survey of European fossil reefs by Toomey (1981) they play an insignificant role, and they are mentioned as encrusters only by Flügel (1981: 291, 316) and Flügel & Steiger (1981). Scattered records, however, indicate that they can locally produce significant amounts of carbonate. For example, Milliman (1974: 117) and Pendlebury & Dobson (1976) mention a contribution of 10–11% to the carbonate fraction in locations on the continental shelves of the eastern United States and Scotland. Hagmeier (1930: 31) states that almost 27% of the sediment in a gully near Helgoland (Germany) consisted of tube fragments of the locally abundant, encrusting serpulid *Pomatoceros triqueter*. Buzhinskaja (1991) reports that in places 30–60% of the 'biomass' in the Sea of Okhotsk may be formed by *Crucigera zygophora* (as *Serpula*).

Several authors have commented upon the ambiguity of the term 'reef'. The accumulated confusion was reviewed and structured by Heckel & Jablonski (1979). In their terminology, a **bank** is an accumulation of carbonate without positive topographic relief, whereas a **buildup** has such relief. If, in addition, there is "evidence of potential wave resistance or of turbulent water, implying wave resistance, and evidence of some degree of control over surrounding environments", then the term **reef** is applied. A subdivision of six types of reefs is given. This paper tries to follow Heckel & Jablonski.

Most serpulids are considered to be 'secondary frame builders', filling crevices and cementing rubble in coral reefs (Schroeder & Zankl 1984; Scoffin & Garret 1984). They act as pioneer organisms (Rasmussen & Brett 1985), but their role is relatively modest (cf. Choi & Ginsburg 1983). However, some Recent species may be regarded as 'primary frame builders', or to use Heckel & Jablonski's (1979) terminology 'welded frame-builders'.

The tube morphology still is incompletely known. Nevertheless, many records of Recent and fossil 'serpulid' buildups can be referred to algae, vermiform 'gastropods', vermetid gastropods or different groups of non-serpulid polychaetes.

Several Jurassic-Cretaceous limestones in NW Germany consist mainly of small calcareous tubes, the remains of serpulids. Accordingly, the limestones have been called 'Serpulit' in German literature. They occur in beds up to 30 metres thick. Recent buildups of serpulids ('reefs') are known from several places, all over the world. However, "little has been done with the ecology of serpulid reefs to date" (Boucot 1981: 91); it is the theme of the present paper. Jurassic-Cretaceous, German, and Recent, Irish 'reefs' were visited by one of us (PvdH), and information on other fossil and Recent serpulid buildups was reviewed, in order to attempt a reconstruction of the palaeoenvironment in which the German serpulid limestones were formed.

1.2. Systematics

Tube-worm is a rather general name for worms living in a tubular housing, and belonging to different taxa of the class Polychaeta (Annelida). Fauchald (1977) distinguishes 17 polychaete orders, of which the Terebellida and the Sabellida are the main tube constructors; some families of the Spionida and Eunicida may also build tubes. Tubes may be chitinous (Chaetopteridae) or parchment-like and covered with silt or other grains (Onuphidae, Ampharetidae). They may be built from silt or sand (Maldanidae), coarse sand (e.g. Pectinariidae and the reef-building Sabellariidae) or shell fragments and other particles (Oweniida, Terebellidae). In Sabellidae, tubes may be gelatinous or semihardened mucous to chitinous and sometimes reinforced with fine sand. One recently described genus of this family has a calcareous tube (Perkins 1991). The morphology of calcareous dwellings constructed by *Dodecaceria* (Cirratulidae) needs further study (section 1.5.2). The same holds for the furrows gradually changing into calcareous tubes reported for the commensal of molluscs *Polydora commensalis* (Spionidae) by Dauer (1991: 607).

Worm tubes of calcite and/or aragonite are almost exclusively produced by the Serpulidae (Order Sabellida). The chemical composition of some worm tubes was studied by Vinogradov (1952: 235–242) and Mitterer (1971); a survey of the ratio calcite-aragonite in serpulid tubes was given by Bornhold & Milliman (1973).

The family Serpulidae contains about 70 Recent genera, which are traditionally placed in three subfamilies : Filograninae, Serpulinae and Spirorbinae. The validity of this classification, and the recent elevation to family rank of the last taxon (Pillai 1970; Knight-Jones et al. 1975; Fauchald 1977), has been questioned by Ten Hove (1984) and Fitzhugh (1989: 11). Unless stated otherwise, the serpulids mentioned in this paper belong to the traditional subfamily Serpulinae. Only current names have been used. Original author, year of publication, original binomen, and synonyms are given in the Appendix.

1.3. Serpulid ecology

Serpulids are represented in a wide variety of aquatic habitats in salinities up to 55‰. Most living taxa are marine. Only one living species is known from fresh water: *Marifugia cavatica*; it occurs in karst caves in Bosnia-Hercegovina.

After a free-living stage lasting from a few hours as (semi)benthos in spirorbids up to two months as plankton in some planktotrophic taxa, the larvae settle and start building a calcareous tube. Tube production was studied by Faouzi (1931), Robertson & Pantin (1938), Swan (1950), Hanson (1948), Hedley (1956a,b, 1958), Vovelle (1956), Neff (1968, 1969, 1971a,b), Finley (1971) and Nott & Parkes (1975). A summary of the process is given by Clark (1976). In the majority of serpulids (99%), the tube is firmly cemented to almost any hard substrate. Only the species of the genus *Ditrupa* have throughout life unattached tubes, on a soft substrate. They resemble scaphopods, especially of the genus *Cadulus*, and as a result both taxa have often been confused (Ten Hove & Smith 1990).

One as yet undescribed species of the genus *Serpula*, from the Canary Islands, may settle on small objects and subsequently keep up with heavy sedimentation. It forms up to 20 cm-long tubes in the coarse sand of its habitat, apparently unattached (Ten Hove, unpublished data). Larvae of *Serpula crenata* most likely settle on small objects too, but the tubes become detached secondarily. They then resemble hexangular scaphopods, although they are somewhat irregularly twisted and not as regularly shaped as a *Dentalium* (Ten Hove & Smith 1990).

The worms extend a number of feathered radioles out of the tube (Fig. 2D). These are used for respiration and suspension-feeding (Hall 1954; Dales 1957; Dixon 1977: 281). The commonly applied term 'filter-feeding' implies a selection of particles according to size or quality, which has not yet been proven for most serpulids. Hence the term suspension-feeding is preferred. When disturbed, the radioles are withdrawn into the tube. In most species the tube opening can be closed with an operculum, a modified radiole, warding off predators. In species occurring intertidally, a tightly fitting operculum may prevent desiccation.

Tubes, especially of juvenile worms, may grow rapidly. Paul (1937) for instance, reports 14 mm in 9 days for *Hydroides elegans*. The growth rate generally slows down at later life stages. In *H. dianthus*, the first three months show an increase in length of 54 mm; in the next 9 months only 12 mm are added (Grave 1933). The growth rate also may depend on temperature and/or population density (e.g. *Ficopomatus uschakovi*, as *Mercierella enigmatica*: Straughan 1972: 118, 120), available food (*Pomatoceros triqueter*: Føyn & Gjøen 1953), and salinity (*F. enigmaticus*: Soldatova & Turpaeva 1960; Turpaeva 1961). In summary, growth rates vary from 1 mm–4 cm per month depending on conditions; 1–2 cm/month is not unusual.

Little is known of the rate of (bio)erosion of the tubes. Tubes may be attacked by boring fungi and algae (Wilson 1976; Bosence 1979: fig. 4; Zibrowius & Ten Hove 1987: fig. 6B), by sponges (Bosence 1979; Rasmussen & Brett 1985), and by crabs and polychaetes (Haines & Maurer 1980a,b). They also may dissolve. On the one hand, Straughan (1971, 1972: 121) states that tubes of *Mercierella enigmatica* (probably an erroneous identification of *Ficopomatus uschakovi*) are disintegrating in 4–9 or at most 18 weeks in the almost fresh water with low calcium concentrations in Brisbane River (Queensland, Australia). On the other, Baudet et al. (1987) found recognizable tubes of *Pomatoceros* in the Loire estuary (France), which had been formed more than 40 years before. From the ratio inhabited/uninhabited tubes of *Pomatoceros triqueter* near Helgoland (North Sea), Klöckner (1976b: 381) concludes that empty tubes will soon be demolished by natural causes. Encrusting tubes in cryptic reef environments are rapidly eroded (Martindale 1976: 103). Juvenile tubes can be completely abraded within one month (Klöckner 1976b: 368). Evidently, erosion depends on local factors.

Vuillemin (1965: 22–37) and Hartmann-Schröder (1967) studied the tube morphology of *Ficopomatus enigmaticus*, known from numerous temperate to sub-tropical localities around the world (Ten Hove & Weerdenburg 1978). This species flourishes in mixo- and hyperhaline waters of subtropical temperatures (salinity terminology according to Anonymous 1958). Growth may then be 30 mm in only 16 days (maximum length is about 100 mm), and tubes are formed with coarser transverse growth lines and with peristomes (flaring tube mouths, Figs 5D, 6B) at irregular intervals. Under less favourable conditions the species forms tubes with finer growth lines and without peristomes (Fig. 6A). Sometimes several peristomes are formed during one summer season. Both endogenic and environmental factors may be responsible. There is some evidence that peristomes are formed simultaneously in certain aggregates, according to Hall (1954) due to shortage of food, but on the whole the formation of peristomes is unpredictable (Dixon 1977: 400). Hargitt (1912) already observed that growth rates of individuals within a given aggregate of *Hydroides elegans* are erratic, not synchronized. According to various authors (e.g. Bianchi 1981: 132), tubes of *F. enigmaticus* encrust the substrate under unfavourable conditions, and do not grow erectly. These adnate tubes have a low longitudinal keel and no peristomes. However, experimental fouling studies (Arias & Morales 1969: pls 1–7; Arakawa 1971: pl.9) have shown that moderate larval settlements result in tubes that are encrusting, rather than erect. Only a dense settlement will force the tubes away from the substrate and give rise to parallel erect tubes (Ten Hove 1979b). This can be effected by mass survival of metamorphosing larvae and sufficient food supply only. If mass settlement and survival are seen as reflecting 'favourable conditions', then erect masses of tubes reflect such conditions by implication (see gregariousness, section 2.2). Individual species may show different growth strategies within a single lagoon, viz. Mar Piccolo, S Italy: *Serpula vermicularis* encrusts in the *Cardium-Balanus* facies but forms erect reefs around submarine springs, whilst *Hydroides elegans* forms small erect aggregates in the *Aloidis-Chlamys* facies (Mastrangelo & Passeri 1975: 2027).

Serpulids normally occupy only a small anterior part of their tubes, but may move deeply inside when disturbed. They do not leave their tubes voluntarily. If forced out, they cannot build a new tube (e.g. Vuillemin 1954b) and will soon die. It still is not clear how a schizont, formed at the posterior end of individuals in some genera, gains access to the outside. Mörch's tentative inference that the parent ('nurse') leaves the tube in order to make way for the schizont (1863: 364), is uncorroborated. His conclusion that *Filograna* (subfamily Filograninae, as *Filigrana*) is the only worm capable of leaving its tube, was taken out of the context and misunderstood by Schmidt (1955: 15).

The life span of individual spirorbids is a few months at most; in larger worms, for example *Ficopomatus enigmaticus*, it may be 4–8 years (Ten Hove 1979a). For the even bigger members of the *Spirobranchus giganteus*-complex, a life span of 30 or more years can be calculated, comparing the lengths of the embedded tubes with the growth rates of the surrounding corals.

1.4. Tube morphology

1.4.1. Serpulids

It is difficult to design a taxonomy of fossil worm tubes since they have a limited number of characters and present little information about their one-time inhabitant. The taxonomy of Recent serpulids is based on the animal rather than on its tube (Ten Hove & Wolf 1984: 55–2). A fleshy, chitinous or calcareous operculum may be present. It is generally lost in fossilization, although some calcareous opercula could be matched with their Cretaceous tubes (Cupedo 1980a, b). Little attention was paid to the tubes in zoological literature, probably partly due to the fact that environmentally induced variation may be great within one species and sometimes even within a single specimen (e.g. Petit & Rullier 1952: figs 1–2; Zibrowius 1968: pl.5 figs 1–19; Ten Hove 1973: pl.IIb, 1975: 63, pl.7a, g; Imajima 1978: fig. 3j). Environmental, ontogenetic and diagenetic changes are still imperfectly documented. In closely related Recent species, for example the 80 species currently recognized in the genus *Hydroides*, most tubes are indistinguishable (Ten Hove 1979a). The few species of this genus co-occurring within a single habitat, however, may sometimes be distinguished by their tubes. On the other hand, species of *Filogranula* are mainly distinguished by their tubes. All this adds to the difficulties in interpreting the fossil record. Palaeontologists can only describe the calcareous tubes and, rarely, opercula. Tracing the present-day relatives poses problems (cf. Regenhardt 1961; Lommerzheim 1979; Jäger 1983). A new technique may help to solve these. Shell growth essentially proceeds in a matrix of organic macromolecules, between which the calcite or aragonite crystals are formed (e.g. Dixon 1980). These macromolecules, still present in fossil material, can be identified with immunological techniques, enabling taxonomic interpretations (Westbroek et al. 1983).

Many, though not all, serpulid tube-walls consist of an outer layer with a series of anteriorly directed chevron-like lamellae, like a pile of plastic coffee cups. In addition, most forms show an 'inner compact layer' or 'cylindrical layer', which is thin, hyaline, and laminated (Götz 1931; Avnimelech 1941; Wrigley 1950; Schmidt 1951; Sokolov 1962 (1971); Milliman 1974; Burchette & Riding 1977; Lommerzheim 1979; Jäger 1983; some of these authors merely copied earlier work). An unidentified fossil serpulid with the same arrangement of tube wall is explained differently by Bandel (1986: pl.10 fig. 4). Thin sections of *Ditrupa* tubes show an inner chevron layer and an outer prismatic layer (Cheng 1974; Ten Hove & Smith 1990). It is not clear whether this inner chevron layer is homologous with the outer ditto in other serpulids or not. The inner chevrons are not mentioned by Bandel, nor visible in his picture of *Ditrupa* (1986: plate 10 fig. 3). Bandel called the outer prismatic layer "false 'crossed-lamellar structure'" (1986: 76), a confusing terminology, probably because he referred to the individual prisms of the first order, wall-perpendicular, prismatic layer seen under a high-power magnification. These prisms then show sheet-like crystals, obliquely aligned (cf. Zibrowius & Ten Hove 1987: fig. 3c; Ten Hove & Smith 1990: fig. 34), resembling a crossed-lamellar structure at a second order level (M.J. Weedon, pers. comm.). It is hard to visualize how the model of tube calcification presented by Clark (1976: fig. 2) could explain at the same time an inner chevron-like structure and outer prismatic layers, or alternatively an outer chevron-like structure and inner laminated layers. Besides, recent SEM work on fractured tubes of the genus *Pomatoceros* by Bubel et al. (1983), and on the genera *Ditrupa*, *Laminatubus*, *Neovermilia*, *Placostegus* and *Protis* by Bohnné Havas (1981), Ten Hove & Zibrowius (1986) and Zibrowius & Ten Hove (1987), has shown that the structure of serpulid tube-walls is more variable than generally assumed. It may even consist of three layers, an arrangement thought to be typical for Vermetidae (Gastropoda) by Barash & Zenziper (1985: 147). Observations from thin sections and from SEM are not easily compared. Moreover, fossils may be recrystallized, rendering structure no longer visible (Lommerzheim 1979: 126). A review based on ample material, and not on literature alone, is necessary.

Some serpulid taxa form internal septa, generally as a response to damage of the posterior tube (Lamarck 1818: 362; Swan 1950: 289–290; Hedley 1958). These oblique septa are characteristically perforated (e.g. Hedley 1958: fig. 11; Ten Hove 1973: pl.I c; Ten Hove & Jansen-Jacobs 1984: 167, 172). Even when in older septa the perforations are filled (Bandel 1986: 68, pl.9), they still are indicated by more or less regularly placed depressions.

Serpulid tubes never have a coiled 'protoconch'. Even the spirally coiled Spirorbidae originate in a straight, open-ended tube (Malaquin 1904: fig. 3; Wrigley 1951). Spirorbids typically form small (up to a few millimetres across) tight coils, with a flattened attachment area. Some taxa grow away from the substrate, forming helically twisted tubes, which might be mistaken for vermetid protoconchs. One of these, *Helicosiphon biscoeensis*, is regularly present in fossil and Recent buildups of *Serpula narconensis* (section 2.2.2.2, material studied, Zoölogisch Museum, Amsterdam nrs. V.Pol. 3477, 3478, 3597; Kirkwood & Burton 1988). This may have led Veronov (1958, cited by Pickard 1985) to the erroneous conclusion that the fossil Antarctic serpulid buildups were formed by vermetids.

1.4.2. Vermetid gastropods

The similarity in external appearance between the tubes of vermetid gastropods (and vermiform 'gastropods', section 1.5.3) and serpulids is such that confusion easily arises (e.g. Götz 1931). Gastropods have a spirally coiled protoconch, closed at its beginning (Morton 1965: fig. 1C; Barash & Zenziper 1985: figs 2, 3). According to Bøggild (1930) and Schmidt (1951), vermetid tubes usually show a wall structure with an outer layer of prismatic crystals and an inner laminated or foliated layer. Weedon (1990), however, mentions a more complicated pattern with a combination of crossed-lamellar, nacreous and prismatic structures. Although the tube of serpulids is not always lustreless (contrary to the statement by Barash & Zenziper 1985: 147), it never has an inner nacreous layer like in Vermetidae.

In some vermetid genera, imperforate, anteriorly concave septa occur frequently (Morton 1965; Yochelson 1971). They differ from the oblique, perforated septa occurring in some serpulids. Differences between serpulid and vermetid tubes are summarized in Table 1.

Vermetid 'reefs' have been mentioned from tropical-subtropical regions by various authors (Kempf & Laborel 1968; Safriel 1975; Hughes 1979; Barash & Zenziper 1985). These 'reefs' are bank-like and strong enough to withstand the surf. They form a long-term diversified habitat (e.g. Ben-Eliahu & Safriel 1982), and – relative to the tiny inhabitants – have a major influence on the environment. Thus it is justifiable to speak of reefs. However, Heckel & Jablonski (1979) define six subtypes of reefs, together clarifying the definition of the (higher ranking) term 'reef', and making it unlikely that the thin (up to 15 cm thick) vermetid encrustations on intertidal rock can be called reefs. Both Kempf & Laborel (1968) and Laborel (1980) stress the usefulness of fossil vermetid banks as precise sea-level indicators, as do Flood & Frankel (1989) for intertidal belt-forming serpulids.

1.5. Confusing records of 'serpulid reefs'

1.5.1. Algal-gastropod reefs

Several 'serpulid reefs' mentioned in the literature are not (mainly) built by serpulids. For instance, (Tizard et al. 1885: 138) mention that "large parts of the Bermuda reefs are formed of *Serpula*-tubes". Agassiz (1895), cited in Götz (1931) described these "serpuline reefs" as mainly built by coralline algae, but nevertheless they were commonly cited as 'serpulid reefs' in the literature (e.g. Walther 1893: 674; Verrill 1903; Sokolov 1962 (1971); Ekman 1967: 54; Schumacher 1976: 14; Croneis 1982). Already Darwin (1841, in Barrett 1971: 141) doubted if they were really such reefs. According to Stephenson & Stephenson (1972: 66–67), Ginsburg & Schroeder (1973), Milliman (1974), Safriel (1975) and Hughes (1979), they indeed are algal-vermetid cup reefs, in which serpulids are a minor constituent only. According to Kempf & Laborel (1968), Rathbun's (1879) 'nullipore-worm tube reefs' from Itaparica (Bahía, Brazil), cited by Walther (1893: 674), fall into this category as well.

Focke (1977, 1978) described similar accretions from the Netherlands Antilles, where an ecophenotype of the serpulid *Spirobranchus polycerus* in some places adds significantly to the framework (cf. Ten Hove 1970: 42). Laborel (1980) summarized the usefulness of fossil vermetid benches as sea-level indicators, since they always occur at the same level: the upper level of the infralittoral zone (*sensu* Pérès & Picard 1964) or the lower limit of the midlittoral zone (*sensu* Stephenson & Stephenson 1972).

The 'serpulid reefs' from Corsica, mentioned by Pérès & Picard (1964: 52), have been unmasked as coralline constructions by Zibrowius (1991).

Sigl (1973: 39, pl.1 fig. 3, pl.3 fig. 6) reported 'Serpelriffe' of about one metre in size from a depth of 15–29 m in the Adriatic Sea. His brief description and photographs do not permit identification. Possibly he was dealing with algal-serpulid bioherms.

In the literature, Pearse & Williams (1951) are mentioned as having reported 'serpulid reefs' from off North and South Carolina. However, they state that "the reefs are mostly made of Trent Marl ... Sessile snails and tubicolous annelids are the chief reef builders" (1951: 160). Although the serpulid involved, *Hydroides dianthus*, builds reef-fields in the

Table 1. Comparison of tube-characters of serpulids, vermetid gastropods and vermiform 'gastropods'.

	embryonic tube	lining of lumen	septa, if present	layers in tube wall
Serpulidae	straight, open at both ends	not nacreous	perforate, oblique in lumen	usually two, exceptionally three
Vermetidae	snail-like, closed at one end	nacreous	imperforate, anteriorly concave,	three
Vermiform 'gastropods'	bulbous or helical, closed at one end	?	anteriorly concave, sometimes with perforate projection	juvenile three, adult two

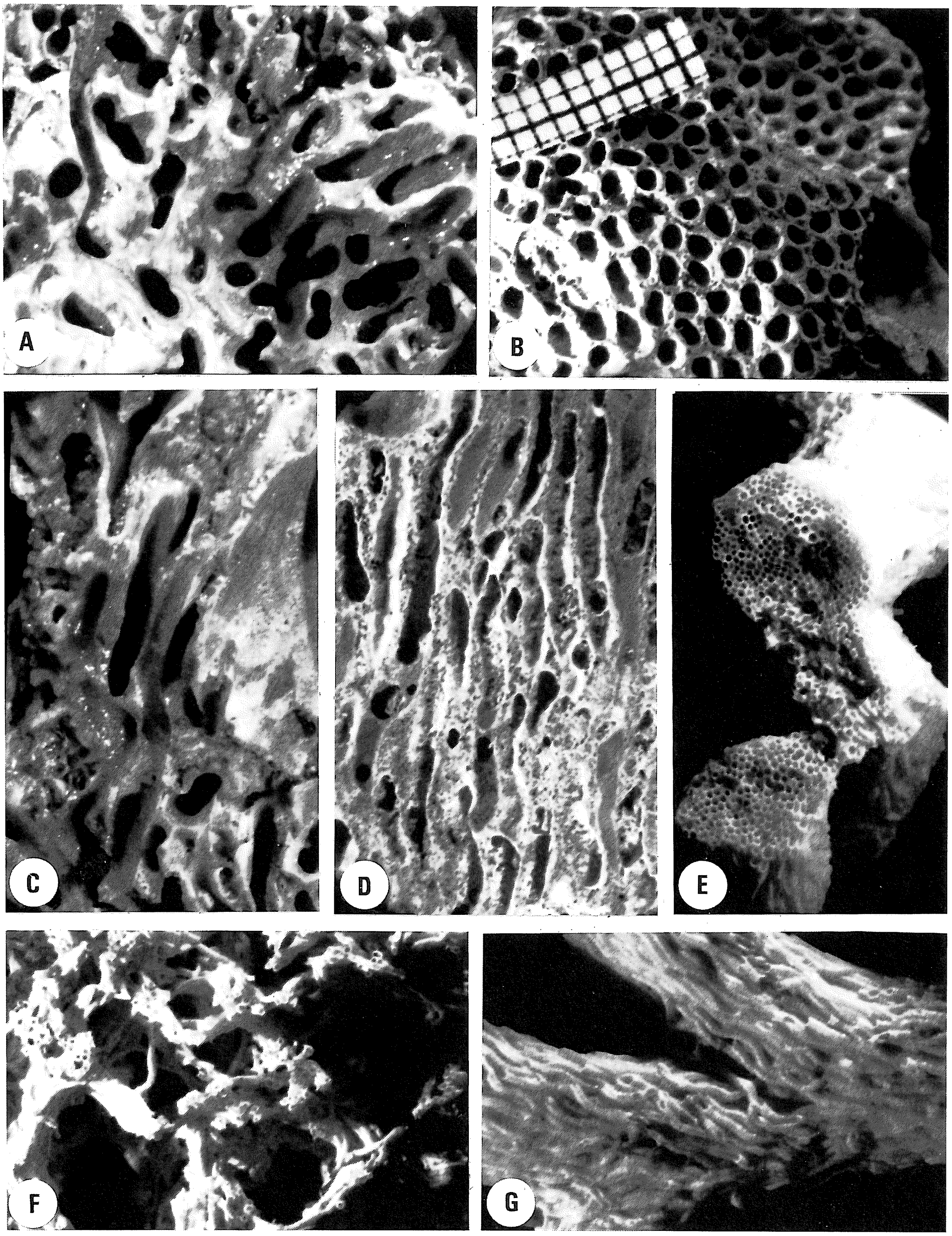

Fig. 1. Tube-clusters. A, C. *Dodecaceria*; more or less transverse and longitudinal cut respectively (Yucatan, Mexico; Recent; Zoölogisch Museum Amsterdam (ZMA) collection number V. Pol. 3803; 3.7 ×). B, D. *Diplochaetetes*, more or less transverse and longitudinal cut respectively (Baja California, Mexico; Oligocene; ZMA V. Pol. 3808; 3.7 ×). E, F, G. *Filograna*. E. Transverse cut, compare Fig. 1G (off Choya, Mexico; Recent; ZMA V. Pol. 3370; 3.7 ×). F. Open meshwork (locality unknown, probably Mediterranean; Recent; 3.7 ×). G. Densely packed tubes, lateral view (same cluster as Fig. 1E).

area (Haines & Maurer 1980a,b), it is evident from Pearse & Williams' text and plates that the large turritellid gastropod *Vermicularia spirata* was the main constituent.

Other records of reef-building serpulids are even shorter and need to be checked, e.g. those of the Quaternary in Crimea (Andrusov 1936: 121), and of the algal-sponge reefs of the Upper Jurassic in S Germany (Schwäbische Alb), described as composed on average of 36% '*Serpula*' (Aldinger 1968, probably referring to the % of number of specimens, not to % sediment weight, *fide* M. Jäger pers. comm.).

1.5.2. Cirratulid patch-reefs

Reish (1952) reviewed two records of '*Serpula*' 'reef-building' from the Plio-Pleistocene of Oregon and California: ?*S. octoforis* and '*S.*' *saxistructuris*. On the basis of a comparison with Recent material from California and South Africa, he concluded that the masses of calcareous tubes had been laid down by the cirratulid polychaete *Dodecaceria fistulicola* Ehlers, 1901, originally described from Chile. Literature on Recent cirratulids is somewhat conflicting. On the one hand, Day, who in 1952 supplied part of Reish's material, maintains (1967: 449) that South African *Dodecaceria* "burrows in thick encrustations of lithothamnion.... How the worm burrows in the dense matrix of the coralline [algae] is unknown but the worm appears to do little damage to the plant which grows up around the hole so that the whole surface is covered with volcano-like knobs." On the other hand, Reish's observations are supported by Hartman (1969: 257 fig. 3), who figured a compact mass of calcareous tubes from California constructed by *Dodecaceria fewkesi* Berkeley & Berkeley, 1954 (probably a synonym of *D. fistulicola*). Mary Petersen (Zool. Mus. Copenhagen, pers. comm.) confirmed that at least some *Dodecaceria* species are capable of making calcareous tubes and of building aggregates of a hard mixture of sand and calcareous cement.

Fischer et al. (1989) and Fischer (1990) studied another (?) patch-reef-building organism, *Diplochaetetes mexicanus* Wilson, 1986, previously attributed to the sclerosponges, from the Oligocene of Baja California and very similar to '*Serpula rectiformis*' from the Eocene-Oligocene of California. On the basis of the skeletal structure, the authors came to a similar conclusion as Reish, namely that their material seems closely related to the modern genus *Dodecaria* (error for *Dodecaceria*).

Recent cirratulid patch-reefs occur near Chicxulub Puerto, NE of Progreso, Yucatan, Mexico. "'Serpulid heads' are locally distributed and spaced along the shore, in a claw-like fashion pointing westward, the direction of the prevailing current. They occur on a flat rocky bottom, veneered with sand and with scattered patches of shoal grass (*Halodule wrightii*), in 2.5–3 m depth and about 150 m off a sandy-shelly shore. These heads are solid hemispherical structures, 0.5–1.0 m in diameter. Only one large living head was observed, whereas most had only small patches of living worms, and were partially covered by a reddish-orange encrusting sponge. The short, black tentacles (3–4 mm) of the worms swayed back and forth with the wave surge giving the heads a 'hairy' appearance" (J.W. Tunnell, pers. comm.). A cursory examination of material from these heads by the senior author revealed black cirratulids (*Dodecaceria* sp. close to *D. coralii* (Leidi, 1855) det. M.E. Petersen), inhabiting a tube-mass (Figs 1A, C) very similar to that figured by Reish (1952: fig. 3), but with its generally short and curved dwellings at first sight unlike the parallel tubes of *Diplochaetetes* (Figs 1B, D; material kindly made available by R. Fischer). Further studies are necessary to ascertain the relation of the various forms mentioned in this section, and the exact way in which cirratulids form patch-reefs.

1.5.3. 'Serpula', 'Spirorbis', and Palaeozoic vermiform 'gastropods'

The similarity in external morphology of serpulids and vermiform 'gastropods' has led to mistaken identifications. Fossil reefs, bioherms and biostromes were reported as 'worm beds', constructed by tubes of *Serpula* cf. *advena*, from the Lower Carboniferous of Cumberland and Roxburghshire, UK (Garwood 1931). Leeder (1973) gave more information of these buildups. Although in his opinion a taxonomic revision is necessary, because of unusual structures unknown in Recent serpulids, he still attributed the buildups to serpulids. However, Burchette & Riding (1977) observed that the tubes have a molluscan wall structure, numerous internal septa and a gastropod protoconch: the tubes would represent a new group of substrate-attached, disjunctly coiled gastropods. The palaeoecology of this taxon was discussed by Wright & Wright (1981). *Serpula helicalis*, reported from the Devonian of Arizona, USA, by Beus (1980) may also belong to this group, although Beus could not find septa in his silicified material.

On the basis of a SEM analysis, Weedon (1990, 1991) disputed Burchette & Riding's attribution of these coiled fossil tubes to gastropods, and argued that the vermiform 'gastropods' belong to the order Microconchida. This order and the enigmatic tubular fossil *Trypanopora* Sokolov & Obut, 1955 should be included in the class Tentaculitoidea (of uncertain phylogenetic relation) because of their shell structure.

Recent spirorbids never are 'reef-forming'. Nevertheless, records of 'spirorbids' as contributors to fossil 'spirorbid'-algal stromatolites, forming monospecific banks or even 'reefs', are numerous, e.g.: Lower Devonian, New York State (Laporte 1967: fig. 16), Devonian, France (Mistiaen & Poncet 1983), Carboniferous, Belgium (Barrois 1904; Malaquin 1904; Hance & Hennerbert 1980), Upper Carboniferous-Lower Permian, New Mexico, USA (Toomey & Cys 1977), Lower Permian, Germany (Stapf 1971), Middle Buntsandstein, Germany (Zimmermann 1907; Haack 1921: 579), Triassic, W Poland (Peryt 1974, 1975) and Miocene, central SE Europe (Hoernes 1898; Andrusov 1936; Papp 1956).

Palaeozoic 'spirorbid' banks are often reported as having been formed in fresh water (Van der Heide 1956), even though Recent spirorbids are marine, or at most brackish species. Trueman (1942) held the view that "these non-marine Spirorbids may have been different from those which occur in marine deposits". Weedon's attribution of many of these records to the Microconchida necessitates a review of all Palaeozoic records of '*Spirorbis*' and other tubular fossils.

Whether true spirorbids or not, 'spirorbid'-algal stromatolites always have been formed in shallow waters, with a high energy level. Occasionally, fossil 'spirorbids' grow on the sides of stromatolitic columns (in Poland, Belgium and France), just as described for Recent stromatolites from Australia (section 3.6.2). However, the Recent animals in general did not actually grow on the living algal mats, but were deposited as empty tubes or tube fragments on the algal mats or between the stromatolitic structures.

2. Recent and fossil mass-occurrences of serpulids

Occurrences of Recent and fossil aggregates of serpulid tube-worms have been summarized by Ten Hove (1979b). Aggregates are nowadays known from about 10% of the 300 Recent species, all occurring singly too and thus not obligatorily gregarious. This implies that serpulid aggregating behaviour is enhanced by environmental conditions.

2.1. Serpulid banks

Recent *Ditrupa* banks have been reported from continental shelves in temperate to tropical seas all over the world (Wilson 1979, Dyer et al. 1982, Ten Hove & Smith 1990). *Ditrupa* banks also are known from the Paleocene-Eocene of N Spain (Gaemers 1978: 190), the Eocene-Lower Oligocene of NW Germany (M. Jäger, pers. comm.) and the Miocene of Taiwan (Cheng 1974, Kilmer 1988) and Victoria, Australia (Ten Hove & Smith 1990), and they are common in the Plio-Pleistocene of the Mediterranean (H. Zibrowius, pers. comm.).

Pendlebury & Dobson (1976) estimate that 11% of the biogenic grains in coarse sands off Scotland is calcareous polychaete (probably *Ditrupa*). In the same area Wilson (1979) ascribes generally 10–25%, locally 50–70% of the total carbonate to polychaete worms. Cheng (1974) supposes that tubes were post-mortem hydrodynamically transported and oriented by bottom currents. Transport, especially downslope, is likely to occur as tubes are commonly found down to about 1000 m. However, living specimens occur mainly above 140 m (H.J.J. Sips, pers. comm.; Ten Hove & Smith 1990). In almost all samples, living specimens are few in proportion to the number of collected tubes (Wilson in Dyer et al.

1982; 'material studied' in Ten Hove & Smith 1990). The maximal percentage of living specimens of *Ditrupa arietina* in populations around Madeira was 58% (H.J.J. Sips, unpubl.). Large samples consisting of mainly living *Ditrupa* are unknown. This suggests that larvae are gregarious, as does the senior author's observation that extensive sampling during CANCAP Expeditions (to the CANary and CAPe Verde Islands; cf Van der Land 1987) provided masses of tubes from some localities, while adjacent samples from similar bottoms showed none. The underlying sediment of the *Ditrupa* masses from Madeira consisted of fine siliceous sand with 40–85% of organogenic calcareous debris (mainly fragments of molluscs and ectoproct bryozoans: H.J.J. Sips, unpubl.). Most probably, banks come into being by the combined action of gregariousness and hydrodynamic transport.

Diester (1972: 47) records a 'Serpellage' (serpulid layer) in one sample from the Persian Gulf, 5% of the sediment consisting of serpulid tube fragments. From Sarnthein (1971: pl. 2 figs 11a, b), working with Diester in the same area, it can be inferred that the main constituent will have been *Ditrupa gracillima*.

The equally bank-forming Cretaceous '*Ditrupa*' *mosae* has been transferred to the genus *Sclerostyla* by Cupedo (1980b). Recent representatives of the latter genus are not known as mass-occurring (Ten Hove 1973). More or less monospecific layers of the square tubes of *Nogrobs* (=*Tetraserpula*) are common in the Middle Jurassic of Germany (M.Jäger, pers. comm.). Tubes of both *Sclerostyla* and *Nogrobs* start affixed, but when growing may soon break away from the substrate. As such they are different from *Ditrupa*, which are unattached throughout life.

2.2. Primary frame builders, gregariousness

An important mechanism in aggregation is gregariousness, defined as "the interactions between planktonic larvae and attached resident members of their own species that result in settlement and metamorphosis of the larvae" (Scheltema et al. 1981). In experimental set-ups, larvae of several serpulid species show affinity for congeneric adults or for the physical environment offered by their tubes (Andrews & Anderson 1963; Straughan 1972; Klöckner 1976a,b; Crisp 1977; Scheltema et al. 1981). Both mechanical and chemical stimuli appear to be responsible for aggregated settlement (e.g. Crisp 1974). Gregariousness in which the physical factors causing larvae to aggregate were excluded was so far only shown for *Galeolaria caespitosa* (O'Donnell 1986: 77–94; section 2.2.2.1).

In this context, the polychaete family Sabellariidae is interesting. Gregarious settlement on conspecific tubes has long been held responsible for the extensive wave-deforming 'reefs', built by members of this family. These may be about 0.5 m high, few metres wide, and several kilometres long (Kirtley & Tanner 1968; Wilson 1971; Gruet 1972). Only recently, however, experiments demonstrated different larval responses for gregarious and non-gregarious Sabellariidae: free fatty acids induced larvae of gregarious taxa to metamorphose, but had no effect on non-gregarious taxa of the same family (Pawlik 1988).

2.2.1. Minor primary frame builders

The only living, obligate freshwater species *Marifugia cavatica* (it dies when placed in mixohaline or salt water) forms aggregates in karst caves in Bosnia-Hercegovina (Absolon & Hrabe 1930). It is widely distributed in the area. Walls and ceilings of subterranean streams are covered with a continuous tapestry, dozens of square metres in area and locally nearly one metre thick, formed by the small worm tubes (8–10 mm long, 0.8–1.0 mm wide). Since the meshwork of tubes (Fig. 2B) is filled in with mud, only the outer layer contains living animals. Penetrating ground water and condensation keep the tube crust wet, even during summer when the streams have dried up, and allow the worms to survive. Placed in water, all animals become active again (Remy 1937; Dizdarevic 1969). The surface of the tapestry of tubes being an open meshwork, the anterior ends of the tubes break off easily and may be deposited elsewhere to become a breccia (cf. Fig. 2A).

A new 'reef-building' serpulid, *Filogranella elatensis*, was described by Ben-Eliahu & Dafni (1979, figs 1, 2a, b), from a crevice in a coral knoll at 3–4 m

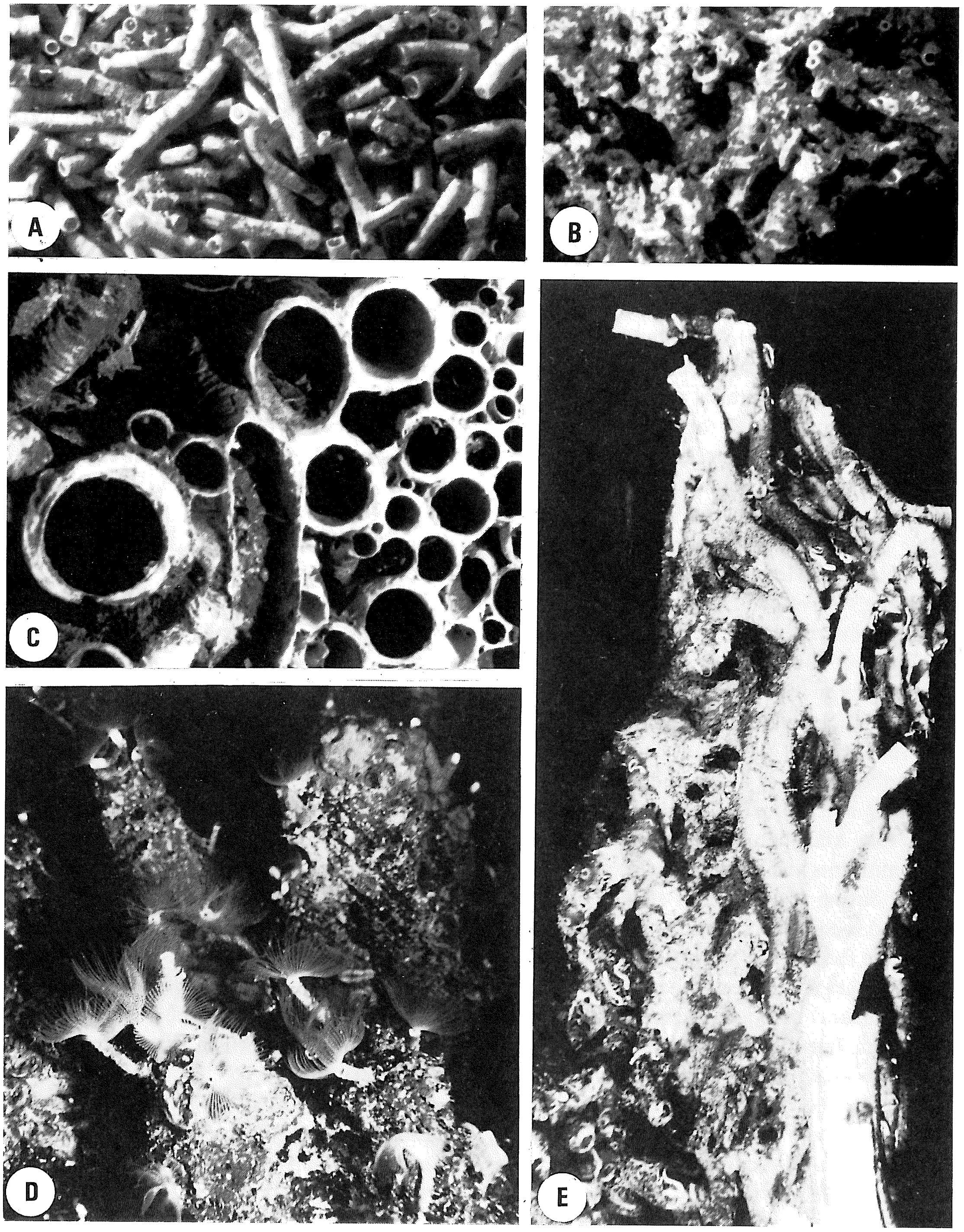

Fig. 2. A, B. *Marifugia cavatica* A. Washed out tubes. B. Individual tubes are hardly distinguishable in the cluster owing to calcareous mud (both Popovopolje, Bosnia-Hercegovina; Recent; ZMA V. Pol. 3103, 3102; 3.7 ×). C. *Serpula vermicularis*, transverse cut through fragment of reef head showing one full grown tube and several smaller ones attached parallel to each other. See also Fig. 3E (Ardbear Lough, Ireland; Recent; ZMA V. Pol. 3780; 3.7 ×). D, E. *Protula tubularia* (?). D. Several living specimens forming pseudostalagmites in cave. Note "hummocky" appearance of aggregate. E. Detail of pseudostalagmite, showing almost parallel growth of tubes and ensuing massive built of aggregate. Smaller tubes belong to other genera of serpulids (Cyprus; photographs S. Weinberg; 0.28 ×, respectively 1.1 ×).

depth, ca. 100 m northwest of the outlet of the cooling system of the Elat desalination-power plant in Israel. This outlet released water of increased temperature, salinity and heavy metal contents. The monospecific worm aggregate had a base diameter of 1.5 m, and a maximal height of 0.6 m. During a recent visit (Ten Hove and Ben-Eliahu, June, 1990) it could not be found again. The same *F. elatensis* or a similar species forms monospecific aggregates of several cubic decimetres on coral reefs in Indonesia, Australia, and Curaçao (Netherlands Antilles), at a depth of 5–15 m (Ten Hove, unpubl.). The discovery of these aggregates under unpolluted conditions, necessitates a reappraisal of Ben-Eliahu & Dafni's opinion that the 'reef' formation, at least in part, should be attributed to pollution.

Macintyre et al. (1982) reported serpulid pseudostalactites, built for more than 90% by two species of the *Vermiliopsis glandigera-infundibulum*-group (det. H.A. Ten Hove 1978), from a submarine cave in Belize. Very few tubes contained living worms; these concretions were up to 50 cm long, with a diameter of 30 cm. The calcification processes involved were analysed by Videtich (1986). For this seemingly stable, submarine cave, MacIntyre et al. (1982) suppose that the erratic layering of the serpulids in the stalactites is due to episodic development. "The inner zones of the ceiling (of the cave) may now and then receive renewed water containing nutrients and serpulid larvae as a result of upheaval during severe winter storms or even hurricanes". As the individual tubes are only about 2 mm wide, the formation of a single pseudostalactite will have taken decades to centuries, rather than years. Similar concretions (diameter 20–30 cm, length up to 1 m; Figs 2D, E), formed by *Protula* sp. (probably *tubularia*), occur in a cave in Cyprus (Agios Georgios Island, Cape Akamas, depth 9 m; S. Weinberg, pers. comm.). The hummocky surface of these aggregates may enhance turbulence, and thus advection of food (cf. Knight-Jones & Moyse 1961).

The above-mentioned skeletal knolls of both *Filogranella* and *Vermiliopsis* consist of tightly interwoven tubes like those found sometimes in *Filograna* (Fig. 2E), and are unlikely to be reworked into a major deposit of tube-fragments.

Por & Dor (1975) describe 'serpulid reefs' from a hyperhaline lagoon (45–60‰) near the Gulf of Elat. On beachrock, they found 20 × 20 cm-large, rounded, head-like reef boulders, constituting the main environment of macroscopical life in the pool. Although the serpulid *Vermiliopsis pygidialis* is the main initiator of these skeletal knolls, and maybe is a frame builder as well, thick crusts of algae and ascidians cover the outside, while the inner knoll is gradually eroded by excavating sponges. The encrusting serpulids thus do not contribute much to the final deposit of calcareous matter.

2.2.2. Major primary frame builders

The major primary frame builders can be divided roughly into three groups, each occupying a major type of habitat and consisting of species that are morphologically (and probably phylogenetically) more similar to one another than to the members of the other groups (Ten Hove 1979b).

The first group consists of taxa that form belts in the intertidal zone of open coasts (*Galeolaria*, *Pomatoceros*, *Pomatoleios* and *Spirobranchus*). In the intertidal wave action, it is clearly advantageous that tubes are mutually supporting and form sturdy clusters. The second group is aggregating in quiet mixoeuhaline lagoons (*Serpula*, *Hydroides* and *Vermiliopsis*). The third group lives in mixopoly-mesohaline and/or hyperhaline environments, including lagoons (species of the genus *Ficopomatus*, incl. its synonym *Mercierella*). Lagoons generally have sandy and muddy bottoms; hard substrates for settlement are rare. In this case, the worms may enlarge the suitable areas. Reef heads grow away from the bottom, avoiding intraspecific competition and siltation, and break off in time forming new substrate for settlement.

2.2.2.1. Intertidal belt-forming serpulids

Sizeable buildups of intertidally belt-forming species are mainly found on semi-exposed coasts in S Africa, S Japan, tropical Australia (*Pomatoleios kraussii*, also as *P. crosslandi*), S Australia (*Galeolaria caespitosa*) and New Zealand (*Spirobranchus cariniferus*, also as *Pomatoceros caeruleus*) (Ten Hove 1979b). They are characterized as serpulid isoassemblages by Pérès (1982: 404–405). Depending on the steepness of the shore, the masses of tubes may occupy a belt of 40 cm to several metres wide, and up to 50 cm thick, in the midlittoral zone (*sensu* Stephenson & Stephenson 1972). Examples are figured by Dakin et al. (1948: pl. 5 fig. 2), Knox (1953: 205 pl. 15.3), Stephenson & Stephenson (1972: figs 8.7, 11.19), and McInnes (1976: fig. 1).

One of the first records of intertidal belt-forming serpulids may be that of '*Serpula lithogena*' from the Baie de Bougainville, île Decrès (Péron [& Freycinet] 1816: 82). Recorded as a *nomen nudum* by Mörch (1863: 453), the name was never mentioned again in the polychaete literature, nor in the literature on worm-like gastropods (R. Bieler, pers. comm.). "Sur divers points de la baie Bougainville, on observait avec admiration des masses très-volumineuses d'une espèce de roche calcaire entièrement formée d'un nombre prodigieux de Serpules entrelacées ensemble". Only the surface contains living worms; no doubt these have smothered their parents below. So far, material could not be traced in the Muséum National d'Histoire Naturelle, Paris, where some of Péron's material can still be found (pers. comm. P. Bouchet and J. Renaud-Mornant). From the locality (île Decrès = Kangaroo Island, S Australia) and intertidal habitat, it is evident that Péron [& Freycinet] were referring to *Galeolaria caespitosa*, described by Lamarck (1818: 372) from Australian material collected by Péron.

A detailed study by O'Donnell (1986: ii–iii), extracted below, on the zonation pattern of *Galeolaria caespitosa* may exemplify similar intertidal belt-forming elsewhere. "More worms recruited within the *Galeolaria* zone than outside it, ... even when the intensity of recruitment was great... Larvae were shown to settle gregariously, ... in greater numbers on dense patches of live adults, suggesting that the agent responsible for the gregarious behaviour was more effective when adults were dense. Some worms did settle on artificial substrate, suggesting that presence of conspecifics is ... not required... Grazing gastropods reduced settlement and survival of young worms on bare rock, but not of worms that settled among the tubes of adults. The gastropods probably damaged the worms while grazing... Most young worms transplanted upshore to areas where water did not form pools died... There was no evidence that any predator caused a significant decrease in the population... It appears, then, that the downward extension of the worm zone is prevented primarily by failure to settle, possibly due to lack of sufficient cues provided by adults, or other causes."

Belt-forming in *Pomatoleios kraussii* was mentioned by Day (1969), Straughan (1967, 1969), Crisp (1977) and others. The causes of zonation might differ slightly from place to place. In Hawaii, worms settling above the range of adults were eaten by crabs, while those settling below were overgrown by colonial ascidians (Straughan 1969). In the Persian Gulf, the cause of death for those settling above the level of adults is unknown, while those settling below were overgrown by ectoproct bryozoa, sponges and filamentous algae (Mohammad 1975).

Flood & Frankel (1989) advocate the use of the maximum height of such intertidal belt-forming organisms as precise sea-level indicators. They found fossil *Galeolaria caespitosa* in a cave '1.02 m' above the upper limit of their modern living equivalents, in New South Wales, Australia. The radiocarbon-dated material suggests that the sea-level was about one metre higher at 3420 BP. A record of Withers (1932) should be reviewed in this light. A mass of '*Serpula*' is present on the piece of limestone with the type specimens of the barnacle *Octomeris crassa*, found "considerably above high-water mark". He states that "they represent a comparatively recent deposit, possibly of Pleistocene age". The bluish tubes of the species involved (Queensland Museum nr. F2026; Magnetic Island, near Townsville, Qld, Australia) are undistinguishable from Recent belt-forming *Pomatoleios kraussii*.

The intertidal belt-forming species all form very closely packed bundles of tubes, mostly cemented for almost their entire length to conspecifics (Figs 3A–C). It is unlikely that erosion would loosen these aggregates to such an extent that the ensuing deposit would consist of single tubes mainly, as in the German 'Upper Malm' serpulid limestones (section 3.4).

2.2.2.2. Mixoeuhaline and euhaline habitats.

Ardbear Lough, Ireland. Reefs, built by *Serpula vermicularis* were first mentioned by Bosence (1973) from Ardbear Lough, and thoroughly de-

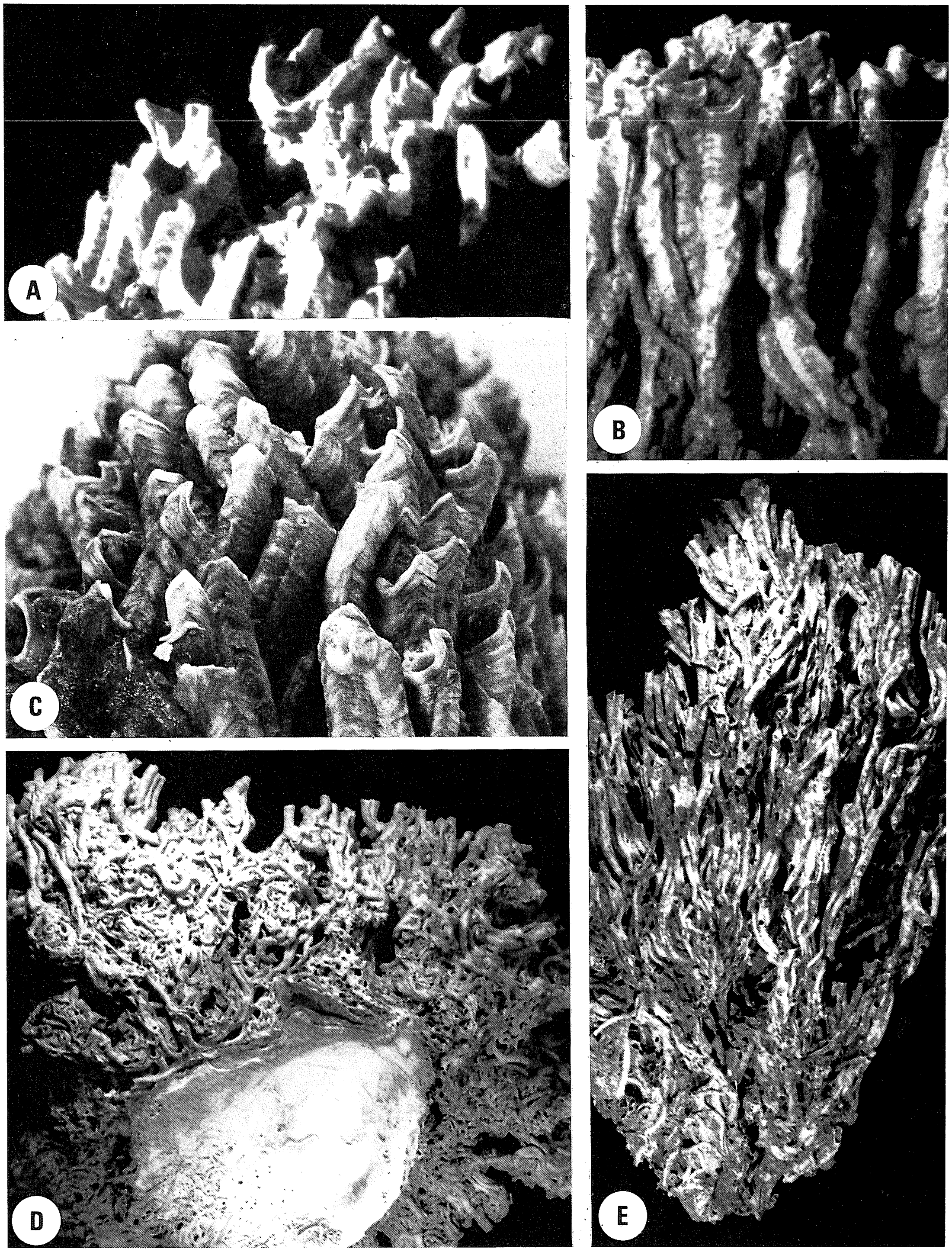

Fig. 3. Tube-clusters of various Recent serpulid species. A. *Pomatoleios kraussii* (False Bay, South Africa; ZMA V. Pol. 3639; 3.7 ×). B. *Galeolaria caespitosa* (Port Jackson, Australia; ZMA V. Pol. 3637; 3.7 ×). C. *Spirobranchus polycerus* (Conset Bay, Barbados; ZMA V. Pol. 3017; 3.7 ×). Note convergence in shape of tubes in the three intertidal belt-forming species (Figs 3A–C). D, E. *Serpula vermicularis*. D. Tubes encrusting an oyster-shell and growing upwards distally (unknown locality; 0.28 ×). E. Fragment of reef head (Ardbear Lough; same sample as Fig. 2C; 0.28 ×).

scribed by him in 1979. His findings are summarized below. Such reefs have been reported too from nearby Killary Harbour (Minchin 1982). Ardbear Lough is a glacially formed lagoon south of Clifden, County Galway, Ireland. Its surface area is about 0.4 km^2. Though mostly shallow, its maximum depth is 30 m. It has a very restricted opening, causing a small tidal range (max. 1 m), and a water exchange with the outside Ardbear Bay of only about 10% per tidal cycle. During spring tides, the Lough gradually fills up with sea water, and salinities range from 25.0 to 33.8‰. During neap tides, the Lough progressively empties. The influx of fresh water from inland drainage systems causes a layering of the water column, resulting in salinities ranging from 5.0‰ in the top layer to 33.2‰ in the deeper parts. The substrates consist for 65% of mud, 25% serpulid reefs and carbonate gravel and 10% rock outcrops, terrigenous pebbles and gravels.

The sublittoral reefs cover areas up to hundred metres across and are mainly initiated on rocky substrates, between 2–20 m depth. After an encrusting stage on a freshly colonized substrate, the worm tubes grow upwards (cf. Fig. 3D). New larvae settle on these erect tubes (Figs 3E, 2C), thus forming large bushes of up to one metre in diameter, and a height of two metres. Around the reef heads, the tube openings show an even (non-random) distribution, generally with a spacing of 10–15 mm. In this position the branchial crowns will not overlap or interfere, and as a result many anterior tube ends are free to lengths of up to 1 cm, not attached to other tubes. As growth of the reef head proceeds, its old base is weakened, mainly as a result of biological erosion by boring sponges and algae, and by grazing fish and echinoids. Consequently segments of the reef fall off, providing new areas for larval settlement. This is the main way by which a reef can expand from its initial rocky outcrop and cover large areas of previously soft substrate.

Where suitable substrates are present throughout, a depth zonation of the reef heads is evident. The maximum development lies between 2 and 15 m. Above this zone brown and green algae are dominant; probably they are stronger substrate competitors than the serpulids. The temporary low salinity in the top layers of the water column may limit serpulid distribution as well. From 15 to 30 m the water is very muddy and has low oxygen levels. These conditions are unfavourable for serpulids (and other macrofauna), as evidenced by transplantation experiments.

The serpulid aggregates are the basis for a rich ecosystem consisting of encrusters like bryozoans, sponges and bivalves, of predators and scavengers like echinoids and fishes, and of species looking for shelter like decapods.

Sediment samples were taken by one of us (PvdH, 18–19 April 1984) between the reef heads at a depth of about five metres. Serpulid tube fragments made up 17.5–60% of the sediment (Table 2).

Plastic pipes of 8.5 cm diameter were driven into the sediment for about 15 cm. Obtaining complete sedi-

Table 2. Taxonomic composition of two sediment samples from between serpulid reef heads (Recent, Ardbear Lough, Ireland); particles larger than 0.85 mm.

Group	sample 1 weight (g)	%	sample 2 weight (g)	%
Serpulids	66.4	17.5%	175.1	59.7%
Bivalves	40.9	10.8%	22.7	7.7%
Gastropods	24.6	6.5%	8.5	2.9%
Balanids	17.2	4.5%	3.8	1.3%
Decapods	0.1	0.0%	2.4	0.8%
Echinoderms	16.8	4.4%	1.1	0.4%
Calc. algae	3.4	0.9%	6.4	2.2%
Rock	123.4	32.5%	66.8	22.8%
Undefined	86.5	22.8%	6.4	2.2%
total	379.4	100.0%	293.2	100.0%

ment cores proved to be difficult. Coring was obstructed by large stones, grasped the upper few centimetres only, and some material was lost during retrieval. The only two sufficiently large and undisturbed sediment samples were washed over a series of standard sieves with meshes from 3.9 to 0.06 mm. All fractions were dried at 80 °C, and weighed. The coarsest fraction of both samples was entirely sorted into nine taxonomic groups (Table 2). The relative weight per fraction was calculated for all groups. Fractions 1.9 and 0.85 were only partially sorted, and results were extrapolated to the whole fraction. Particles of the finer fractions were too small for reliable identifications. In total, 70.6% of the first and 83.7% of the other sample was actually sorted. The ratio 'whole tubes' / smaller fragments was determined in the two coarsest fractions as well; 'whole tubes' were defined as having at least one entire, cylindrical part. Finer fractions only contain smaller tube fragments. Bivalves and gastropods were identified to species level, as far as possible.

In both samples, more than 70% of the particles are larger than 0.85 mm, and the finer fractions contribute little to the total weight (Table 3). Regarding the taxonomic composition of the three coarsest fractions together, serpulids, terrigenous gravel and undefinable particles are most frequently found (Table 2). The three fractions analysed separately show that most serpulid fragments are larger than 2 mm. Molluscs, balanids, decapods and echinoderms are present but of minor importance. Remarkable is the high diversity of molluscs: 17 bivalve and 23 gastropod species. In the fraction coarser than 3.9 mm, 84–90% of the tube fragments still show at least one entire, cylindrical part. These 'whole tubes' are fragments of adult tubes; the maximum tube diameter of *S. vermicularis* is 5 mm. The 25% 'whole tubes' in the 2–3.9 mm fraction are tubes of younger worms.

In fragments of the reef heads, seasonal growth appears not to be reflected in either striation on the tubes or lengths of peristome-intervals.

In conclusion, the aggregation of *S. vermicularis* in Ardbear Lough appears to be induced by a limited availability of hard substrates and a surplus of larvae after spawning, caused by restricted water exchange with the open sea. The total amount of substrate suitable for larval settlement is diminished further by physical factors like mud sedimentation, low oxygen levels and fluctuating salinities. On the other hand, the serpulids create their own settlement sites. Initially, about 5% of the bottom will have been hard substrate; the developing reefs have increased this to about 25%. Moreover, near the mouth of the Lough, carbonate gravels have been deposited which are composed mainly of eroded serpulid reef material, together with some shell debris (Bosence 1979: 305, fig. 7). According to B. O'Connor (pers. comm.), a serious decline in the *Serpula* population over the last number of years affected its structure significantly.

Ellis Fjord, Antarctica. A few years ago, a remarkable example of serpulid buildup was discovered in Ellis Fjord (Vestfold Hills, Antarctica). First mentioned by Perrin (1983, in Pickard et al. 1986), it was described extensively by Kirkwood & Burton (1988) (cf. section 1.4.1). *Serpula narconensis* builds

Table 3. Size fractions of two sediment samples as in Table 2.

fraction (mm)	sample 1 weight (g)	%	sample 2 weight (g)	%
3.96	118.8	22.1%	214.4	61.2%
1.98	94.0	17.5%	49.8	14.2%
0.85	166.5	31.0%	29.2	8.3%
0.71	36.5	6.8%	5.2	1.5%
0.43	82.5	15.4%	11.7	3.3%
0.36	9.1	1.7%	2.2	0.6%
0.30	12.9	2.4%	3.5	1.0%
0.06	16.7	3.1%	22.1	6.3%
<0,06	0.0	0.0%	12.6	3.6%
total	537.1	100.0%	350.6	100.0%

a sizeable reef in 8–30 m depth (diving was restricted to 30 m, but reefs did not appear to go much deeper; J. Kirkwood, pers. comm.). Tube-clusters of up to 2 m in diameter and 1.5 m in height (Fig. 4A) stretch out over a length of more than 8 km. The serpulid covers 25% of the benthic substrate in the fjord down to a depth of 32 m, in many places with a 100% cover. The waters are of normal salinity and have a temperature of 1.4–1.9°C below zero. A possible explanation for this unusually high proportion of suspension-feeders is the high level of primary production in the fjord.

The reefs have characteristics similar to those of Ardbear Lough. They form a substrate for more than 100 other taxa. Their upper limit is defined by the influence of fresh water from melting ice in the summer; the lower limit by sandy substrates or by Porifera (sponges) and Ascidiacea (tunicates). Although the worms show a preference for rocky substrates, they are able to colonize sandy areas too. Dead reef heads, fallen to the bottom, function as substrates for young animals.

Interestingly, the reefs apparently are already present since 7680 ± 120 yr BP. Calcareous banks from this area, with a total thickness of 2.5 m, consisting for more than 50% of loose serpulid tubes, were at first erroneously mentioned as *Hydroides* sp. (Zhang et al. 1983), and as *Mercierella enigmatica* (Adamson & Pickard 1983). They were later identified as *S. narconensis* (Ten Hove, in Pickard 1985). The fossil serpulid tubes occur in two different modes: encrusting pebbles and boulders, or in irregularly bedded deposits of tube fragments, often cemented together in bundles of up to 4 cm long (Pickard 1985: 194–195; Fig. 4C). The diameter of the tubes is up to 3 mm, with a thickness of the walls of 0.05–0.15 mm (our measurements). These beds cannot represent an unmodified in situ aggregation but probably are bundles of tubes which have fallen to the bottom from a fragmented nearby reef.

Baffin Bay, USA. Probably the famous 'serpulid reefs' of Baffin Bay, Texas, USA, mentioned by several authors (Reed 1941; Hedgpeth 1953, 1954; Breuer 1957; Shepard & Rusnak 1957; Mitterer 1971; Milliman 1974; Schumacher 1976; Boucot 1981; Pérès 1982), have also been formed under mixoeuhaline or euhaline conditions. Andrews (1964: 119) argued that Baffin Bay may have been a 'normal salinity lagoon' in the past. He gave a detailed description of the buildups and the environment. Baffin Bay is a drowned river valley system, connected to the north part of the Laguna Madre. Nowadays, the waters are poikilohaline, generally hyperhaline with a salinity range from 1.4–75‰, averaging 51.7‰ during 1951–1953 (Andrews 1964). Salinities varied from 34.5–88.8‰ in the inner parts of the bay in the years 1946–1948 (Hedgpeth 1953: fig. 37). These elevated salinities are due to high evaporation and reduced run-off. Continuous south-east winds cause a permanent high turbidity. Salinities prior to the completion of the Intracoastal Canal in 1946 even soared as high as 102‰ (Breuer 1957), which will have killed any serpulid.

The buildups are only found in shallow waters (0.6–2.4 m) along the bay margins. Two distinct forms of 'reefs' are recognized: patch-reefs and reef fields. The patch-reefs are small, isolated, more or less circular reef heads, 8–40 m in diameter. Cores have been taken from such heads, revealing that they developed on loose sediment of sand and shells. The reef fields are large areas of sandy bottom, covered by broad expansions of scattered reef rock, protruding 40–50 cm above the sediment. The buildups are covered by a thick mat of green filamentous algae and several invertebrate species: barnacles, bivalves, stone crabs and mat-forming bryozoans. On the most inland stations, with the highest salinity values, only some small tufts of green algae are attached to the reef blocks. Material studied by us shows one additional detail (ZMA V.Pol. 3802, made available by W. Tunnell and B. Hardegree, Corpus Christi State University, Texas). The reef heads are not unlike clumps formed by *Filograna implexa* or *Serpula vermicularis*, in the sense that the spatially alternating bumps and hollows enable a maximal number of worms to collect food, and at the same time avoid interference with their neighbours (cf. Knight-Jones & Moyse 1961: 85).

Within the buildups two different growth structures can be recognized: random growth (cf. Fig. 4D) with barnacle-incrustation and oriented growth (Fig. 4B; Andrews 1964: fig. 5). Andrews supposed that oriented growth took place under 'optimum growth conditions' (food, oxygen, tem-

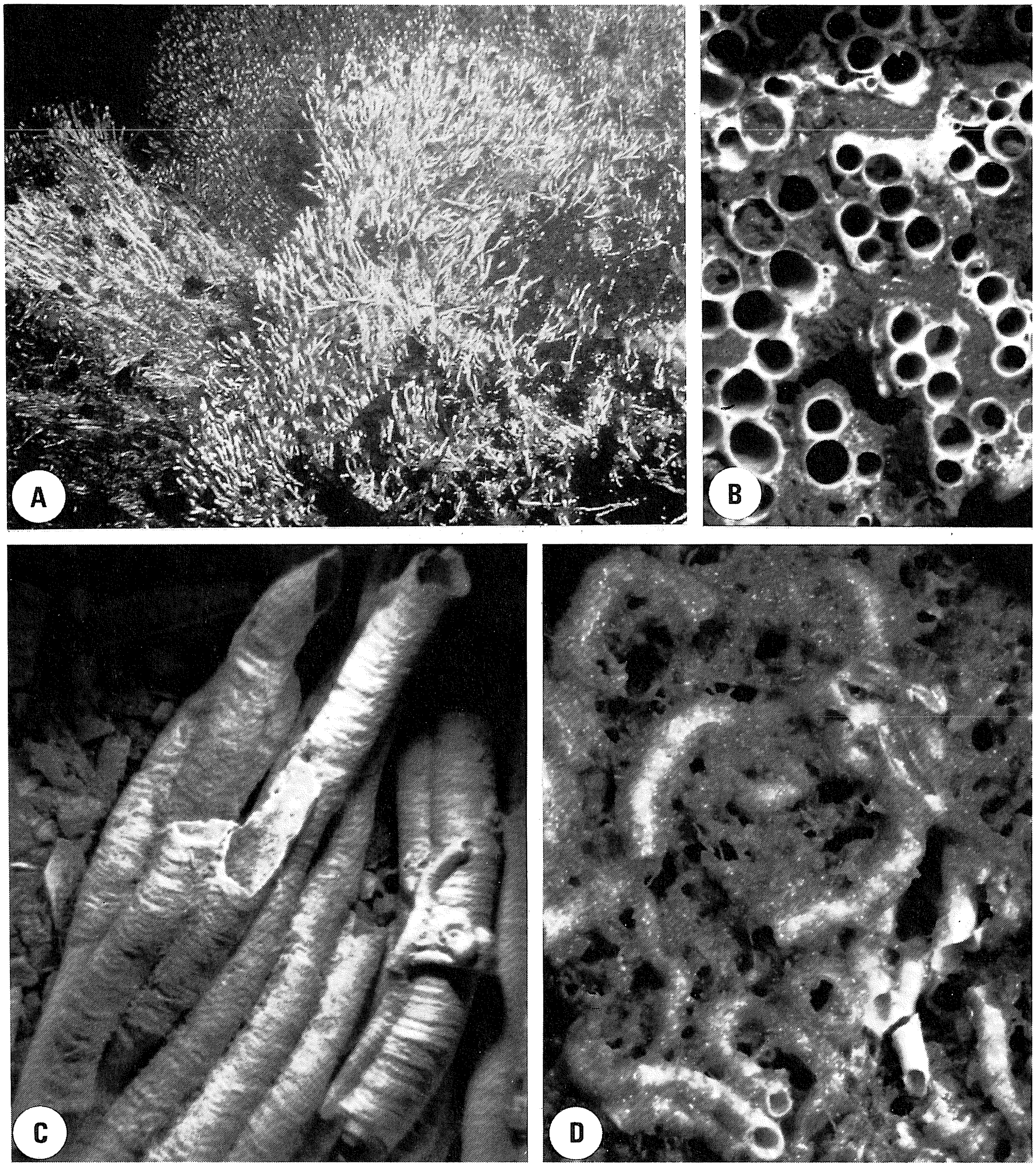

Fig. 4. A. *Serpula narconensis*, reef head (Ellis Fjord, Antarctica; Recent; photograph R. Besso; scale unknown). B. Transverse cut through fragment of subrecent reef head, probably *Hydroides dianthus*, showing parallel tubes (Baffin Bay, Texas; ZMA V. Pol. 3802; 3.7 ×).C. *S. narconensis*, tube rubble (Vestfold Hills, Antarctica; subfossil; ZMA V. Pol. 3478; 3.0 ×). D. *H. dianthus*, tubes encrusting subrecent reef head (same sample as Fig. 4B; 3.7 ×).

perature, calciumcarbonate) whilst random growth occurred under adverse conditions of temperature and/or salinity (however, see section 1.3). Sediment analysis of bottom samples adjacent to the patch-reefs gave for the fraction coarser than 0.72 mm the following weight percentages: serpulid tubes 5–15%, barnacles 15–45%, molluscs 5–10%. The mollusc fraction included four species, of which three are characteristic for sandy and shelly bottoms in high-salinity lagoons.

In recent times no living worms have been observed in the buildups. Hedgpeth (1953: 177) cites a manuscript by W. A. Price (1950), in which active growth of the aggregations was reported between 1875–1910. In 1971 living serpulids were not present (D. E. Harper, pers. comm.). It is unknown which species actually constructed the reefs. Price's material (Allan Hancock Foundation nr.5650, now Natural History Museum of Los Angeles; made available by K. Fitzhugh and L. Harris) consists of several reef fragments of a few centimetres. The constructing tubes show two longitudinal rounded keels, and peristomes are absent. Such tubes occur in many *Hydroides* species, for instance *H. dianthus*. In larger reef blocks (ZMA V.Pol.3802), the tubes do not show free parts, only the diameter and thickness of the walls (Fig. 4B) could be measured. For comparison (Table 4), two populations of *Hydroides dianthus* have been used, respectively from Georgia, Sapelo Sound (ZMA V.Pol.3640) and Florida, Indian River (ZMA V.Pol.3664), as well as *Ficopomatus enigmaticus* from the Lake of Tunis (ZMA V.Pol.3779) and *H. elegans* from Australia (Australian Museum nrs. W3659, W198114). These three possibly reef-forming species have been reported from nearby localities in Texas.

It appears that the differences in tube-measurements between Baffin Bay and *H. dianthus* from Florida are smaller than between the populations of *H. dianthus* from Florida and Georgia. These measurements certainly do not agree with those of the other two species, which show much thinner tube-walls as well as smaller diameters. Nowadays *H. dianthus* lives as an irregular cover of encrusting tubes in the hollows of the dead reef heads (Fig. 4D). It is likely that the subfossil reefs have also been constructed by this species.

A few remarks follow on the other possible reef formers reported for the Baffin Bay area. Ladd (1951: 139) mentions *Chitinopoma* sp. (identified by Pettibone) from the Laguna Madre area. Occurrence of this arctic-boreal genus in subtropical conditions is, however, extremely unlikely, and more easily explained by a misidentification of the similar *Ficopomatus*. The species *F. enigmaticus* has been reported from Rockport in the same coastal lagoon system (Ten Hove & Weerdenburg 1978), and a small aggregate of it was recently collected in Packery Channel, N Laguna Madre (J. Adams and W. Tunnell, pers. comm.). *Hydroides elegans* caused severe fouling in the concrete tunnels supplying cooling water to the power station of Corpus Christi Bay (Behrens 1968), only 50 miles north of Baffin Bay and in open contact with the Laguna Madre. However, so far no natural 'reefs' of this species have been reported, except two records of small 'reefs', probably better termed aggregates, respectively from Mar Piccolo, a lagoon in S Italy (Mastrangelo & Passeri 1975: 2027) and locally in the Lake of Tunis (Zaouali in Harbridge et al. 1976).

Other occurrences. Serpulid assemblages, somewhat less massive than those described above, are built by *Hydroides dianthus* in salinities of 23–28‰ in Delaware Bay, USA (Maurer et al. 1979; Haines & Maurer 1980a, b). The buildups consist of series of narrow (less than 25 m wide), elongate, disconnected tube clusters separated by sediment areas. They stretch out for 500 to 1000 m, in about 6 m water depth, and cover a total area of about 1 km^2. Clusters of tubes range in size from 10 to 400 cm^3, rising 2 to 10 cm above the bottom. The sediment consists of a mixture of poorly sorted very fine, muddy sand with some coarse sand. Mean grain size varies from 2.9 to 4.5 Φ; the silt-clay fraction from 22

Table 4. Comparison of serpulid tube measurements (in mm) for subrecent reef worms of Baffin Bay, Texas, and three Recent reef-forming species. SD = Standard Deviation, n = number of measurements.

Locality	species	diameter of tube (mm)				thickness of tube (mm)			
		range	*mean*	SD	n	range	*mean*	SD	n
Baffin Bay		1.6-2.3	*1.95*	0.23	12	0.2-0.3	*0.25*	0.04	12
Georgia	*H.dianthus*	1.5-2.6	*2.0*	0.36	14	0.2-0.5	*0.31*	0.11	5
Florida	*H.dianthus*	1.9-2.4	*2.18*	0.16	9	0.3-0.5	*0.43*	0.07	9
Australia	*H.elegans*	1.1-1.7	*1.4*	0.20	9	0.05-0.13	*0.08*	0.03	9
Tunesia	*F.enigmaticus*	1.1-1.8	*1.4*	0.25	12	0.05-0.2	*0.13*	0.13	12

to 53%. Fragments of tube heads are incorporated in the sediment. Most typical for these buildups is the abundant associated fauna: over 50 species; 17 of them proved to be statistically dependent on the tube worm. In the reef sediment the gastropod *Mitrella* and bivalve *Nucula* are abundant; many soft-bodied invertebrates occur too. The spatial heterogeneity offered by tubes does increase species diversity, as shown experimentally by Dauer et al. (1982) in nearby Chesapeake Bay.

The 'antireefs', built by *Serpula vermicularis* (and bryozoans) as chalice-shaped frame works around submarine springs in a lagoon in S Italy (Mastrangelo & Passeri 1975) are unique and strictly local. It is not likely that such buildups will be encountered elsewhere.

Serpulid buildups, described from the inner skerries along the Norwegian coast (Gaertner 1958), have probably been built by *Pomatoceros triqueter* (Ten Hove 1979b). They are formed in depths of 3–4 m on the leeward sides of small islands from Harstad up to Tromsö. Subfossil terraces of serpulid limestone, mixed with bivalve grit, are found up to 12 m above sea-level in the same area.

2.2.2.3. Mixopolyhaline and hyperhaline habitats. The Lake of Tunis has been the subject of intensive study (Heldt 1944; Lucas 1959; Vuillemin 1952, 1965; Hartmann-Schröder 1967; Harbridge et al. 1976; Ali et al. 1977; Kelly 1977; De Groot & Ottevanger 1980; Keene 1980). Especially the northern part of this subtropical, seasonally hyperhaline lagoon near the city of Tunis is strongly influenced by man. Due to hydrological works the water exchange with the Mediterranean is restricted nowadays. On average the lake's water contents will be exchanged every 10–30 days. Pollution stems from sewage waters of surrounding communities, and to a lesser extent from cooling water of an energy plant. Eutrophication may be the most severe from all marine waters in the world. Salinity ranges from 28 to 47‰, and temperature from almost 10 to 30°C, with an average of 18°C; the maximum depth is 1.9 m, the pH is 8–9 in general, and 9–10 in the reefs.

Large reef heads, domes or micro-atolls with a diameter of 1 to 3 m, but occasionally up to 750 m in length, are formed by *Ficopomatus enigmaticus* (Vuillemin 1952: pl.14, 1965: 340–345 figs 1–12; Heldt 1953: figs 1–4; cf. Figs 5A–D, 6A–C). Growth of micro-atolls and reefs mainly takes place at their edges; worm-tubes in the centre generally are empty. The reefs are rather fragile, but sufficiently strong to carry a person, at least in the centre of the patch. Altogether about 10% of the North Lake is filled in with worm reefs, with a total mass of carbonate estimated at 540 000 tons of dry weight. The North Lake covers an area of 28 km^2. Its reefs grow up to just below the water surface, thus restricting water circulation. Although in places *Hydroides elegans* and *H. dianthus* are present as well (Zibrowius 1979; Vuillemin 1954a), these species do not play a significant role in the reefs in the North Lake (cf. Harbridge et al. 1976). Bottom sediments are almost anaerobic and consist of very fine mud and some shell gravel, made up of the remains of gastropods (*Hydrobia ventrosa* and *Pirenella conica*), ostracods and barnacles. Other bottom dwellers like the bivalve *Cerastoderma edule* and the gastropod *Cyclope neritea* (as *Nassa*) are also present. The reefs probably started from larval settlement on any small solid object, e.g. pebble, tin can, bottle, brick, as mentioned for similar accretions in the southern U.K. (Thorp 1987; cf. Fig. 3D). Worm tube fragments make up a surprisingly low percentage (less than 5%) of the sand-size sediment, although occasional patches are almost entirely composed of them. They are more abundant in the fraction coarser than sand, usually representing less than 15% of the weight of the sample. Thus most of the $CaCO_3$ content of the sediments (on average 64%, excluding the samples composed entirely of worm reef material) is produced by molluscs, ostracods and forams (Harbridge et al. 1976). Saad (1974) gives an average carbonate content of 63% for the bottom sediments of Lake Mariut (Egypt, Mediterranean), where *F. enigmaticus* is abundant too.

Less well-documented cases of *Ficopomatus* forming 'reefs' are reported from a tidal stream in the Sydney area, Australia (Allen 1953), a hyperhaline lagoon in S Australia (Geddes & Butler 1984; Bone & Wass 1990), the thermally polluted mixohaline harbour of Flushing, SW Netherlands (Wolff 1969; Ten Hove & Weerdenburg 1978; cf. Fig. 5C), lagoons in Italy (Bianchi 1981: pl. 2; Bianchi, Chessa

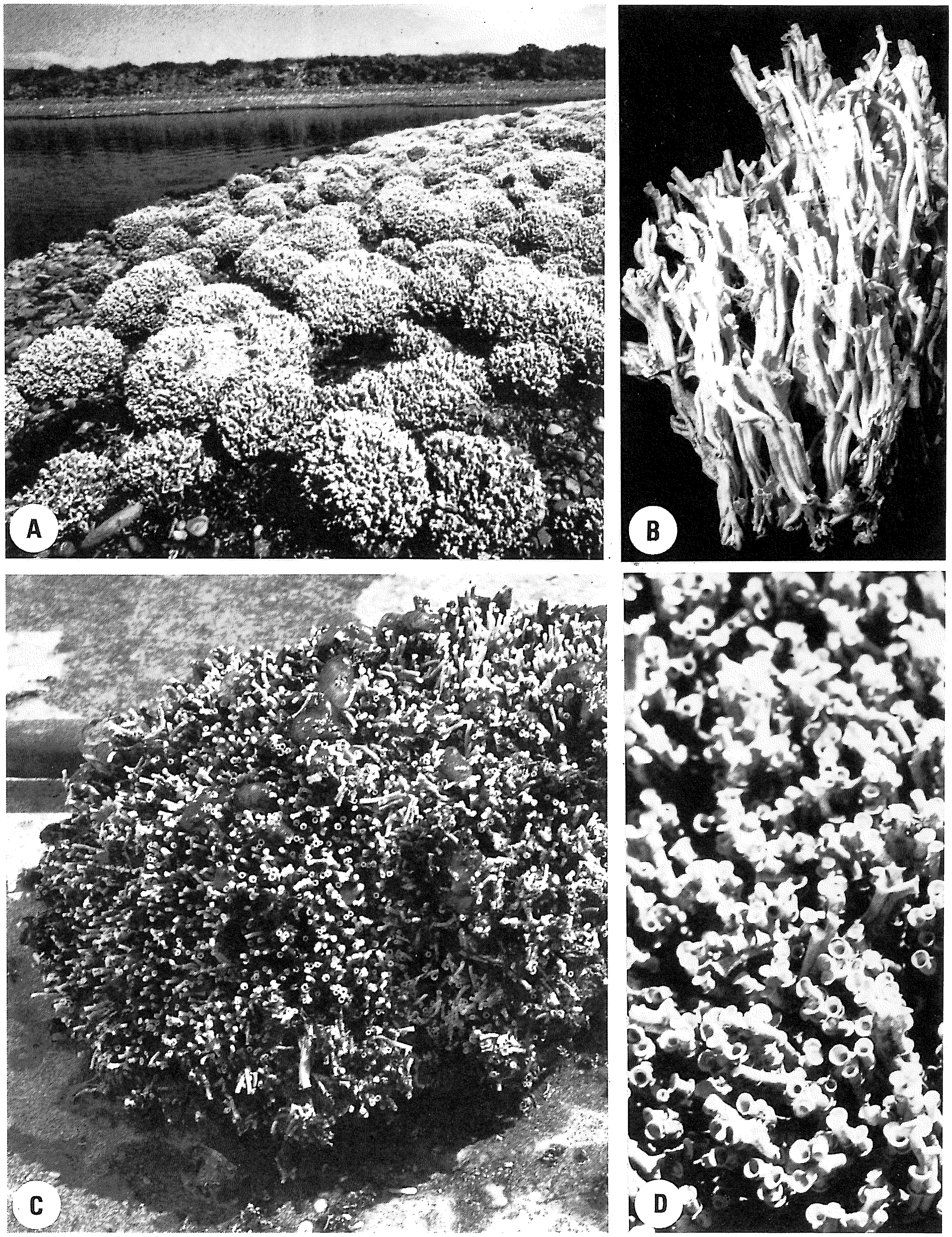

Fig. 5. Ficopomatus enigmaticus, Recent. A. Reef-field emerged at spring tide (Pickleridge Lagoon, Wales; photograph K. Atkinson; scale unknown, but individual clumps will be 30–60 cm across). B. Small fragment of a reef head, oriented growth (Lake of Tunis, Tunesia; ZMA V. Pol. 3779; 0.84 ×). C. Detail of reef head, showing relatively open structure of surface layer (Flushing, the Netherlands; ZMA V. Pol. 3169; 0.33 ×). D. Close-up of Fig. 5A (photograph K. Atkinson; 1.6 ×).

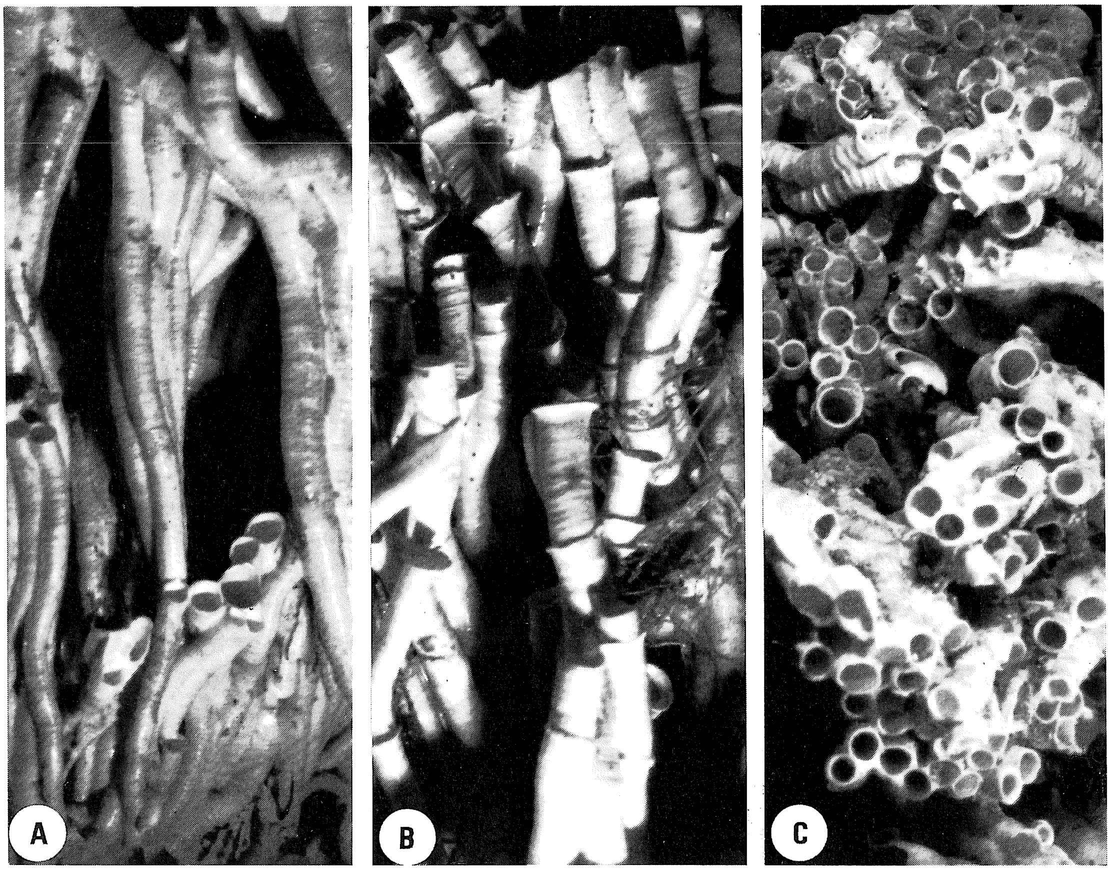

Fig. 6. Ficopomatus enigmaticus, Recent. A, B. Details of Fig. 5C, showing that tubes may or may not have peristomes, depending on their position in one and the same cluster (3.7 ×). C. Transverse cut through fragment of reef head as in Fig. 5B (Lake of Tunis; 3.7 ×).

& Morri 1984; Gravina 1985), the harbour of Martigues, S France (Ten Hove, unpubl.), mixohaline lagoons in S France (Petit & Rullier 1956), and Pickleridge Lagoon (Figs 5A, D) and the docks in Cardiff, S Wales (pers. comm. C. Mettam). The development of such reefs in S England was monitored by Thorp (1987). In these comparatively quiet lagoons, the reefs have a definitely hummocky appearance (Fig. 5A), probably enhancing turbulence and food supply (cf. Valentine 1973: 249; Holloway 1990).

An early Indo-Pacific record, Mahim 50 mi N of Bombay (Keswal 1892), states "*Serpula* builds reefs here that would not be a disgrace to some of the corals". At that time, but later as well (e.g. Withers 1932; section 2.2.2.1), the name *Serpula* was often used for almost any serpulid by non-specialists. The topography of Kelvi-Mahim beach has changed due to land reclamation, and serpulid reefs are not present any longer (U.D. Gaikwad, pers. comm.). In view of the previous presence of a lagoon, and the record of *Ficopomatus* spp. from backwaters in India (Ten Hove & Weerdenburg 1978: fig. 6), Keswal's record is mentioned here.

2.2.2.4. Serpulid buildups from the Tertiary.

In their letter to Sir Charles Lyell, Desor & Cabot (1849, also in Packard 1867) describe a location near Sancati Head, Nantucket (Mass., USA), which in their opinion is of Miocene age. On a layer of tough clay they found an oyster-bank of one foot thick, intermixed and covered by large masses of '*Serpula*', which were, like the oysters, in their natural growth position. The oysters point to a slightly mixohaline palaeoenvironment. Probably they were used as settlement sites, and subsequently smothered by the serpulids. Recent oysters, mussels and whelks, completely covered by tubes of *Pomatoceros triqueter*, are frequently found in the North Sea (Wollebaek 1912: pl. 49; cf. Fig. 3D).

Schmidt (1955: 74) mentions rock-forming masses of serpulids in the Austrian Tertiary, citing Papp & Häusler (1940) and Brandl (1952); further references are given in the Lexique Stratigraphique International (Europe 8). Some of Schmidt's material was studied by the junior author in the Vienna Museum of Natural History. A Tortonian piece (Donau cliffs near Petronell, 1869) has two labels: *Serpula intestinum* Lmk., Rovereto det. and an obviously newer one: *Hydroides norvegica* Günerus (*sic*). It shows great similarity with the Jurassic Lower Serpulid Limestones from the Hannover region in Germany: small, fragmented tubes embedded in a calcareous matrix. Schmidt supposed that these fragments had been secondarily transported. A second piece is labelled "1938 No 36, Serpulid colony (Serpulit) on Lithothamnion limestone, Miocene, Torton-Leithakalk, Mannersdorf am Leithagebirge, *Hydroides norvegica* Gün.". This shows the original growth form. The basis is a pebble of rhodolite (diameter about 8 cm), covered with initial tube-whorls, from which straight, more or less intertwined tubes arise. The growth form is similar to Recent accretions of *H. elegans*, as described by Behrens (1968). The whole pebble is enclosed in a coarse sandstone; probably the growth of the serpulids was stopped by the sedimentation of sand. *Serpula intestinum* **non** Lamarck : Rovereto, 1895 was included in Schmidt's list of synonyms of *Hydroides pectinatus*. Obviously *'H. norvegica'* is Schmidt's preliminary identification of *H. pectinatus* (section 3.5).

Schmidt's Sarmatian pieces from Deutsch Altenburg and Nussdorf are labelled *Hydroides pectinatus*. The small tubes have a diameter of 1 mm, and a length of about 10 cm; the outer surface shows a more or less developed, dense transverse striation. Such serpulid limestones have been found in the Upper Tortonian and Lower Sarmatian from the Vienna Basin and Steiermark in Austria. The Lower Sarmatian limestones were probably deposited in mixohaline environments (Schmidt 1955).

Serpulid limestones have also been reported from the Miocene in Poland (Pisera 1978), and from the Miocene and Pliocene in Spain (Völk 1967; Pagnier 1977; material studied, Geol. Mus. Amsterdam nrs. J5729, Figs 7B, D, G and Pg74 071, Figs 7C, E, H); the latter are layered reef heads, deposited in situ (Pagnier 1977: fig. 2).

2.2.2.5. Serpulid buildups from the Mesozoic.

Serpulid reefs, formed by *Filograna socialis*, occur at the Triassic-Lias boundary in S Spain. The largest is an "irregular body cropping out for some 75 m in length and 25 m in height. Their internal structure consists of three distinct facies: a serpulid/synsedimentary-cement boundstone; a serpulid boundstone, often covered by microbial micritic crusts; and a bioclastic breccia, also at times encrusted by thin micritic laminae". The reefs grew "in a context of micritic and pelitic sedimentation upon a westward dipping carbonate ramp, supposedly below the storm-wave base and outside the influence of strong currents. The 25-metre height of this bioconstruction was reached by the accumulation of successive growth stages that were simultaneously surrounded by sediments and never stuck up above the sea floor more than a few centimetres. The concentration of serpulids attracted an epifauna, mainly brachiopods, which lived on or near the serpulids. In the neighbourhood of the reef invertebrate remains are much more abundant in the same level than further away" (Braga & Lopez-Lopez 1989). The authors conclude that the reef grew in deep water, but still in the photic zone. There is a similarity with the Recent assemblages of *Hydroides dianthus* in Delaware Bay (section 2.2.2.2).

2.3. Secondary frame builders

Most serpulids occur cryptically, in crevices between coral rubble, and may be regarded as secondary frame builders. A special case are the aggregates enhanced by asexual reproduction through scissiparity, reported for three genera by Ten Hove (1979b): *Filogranula*, *Filograna* and *Josephella* (the last two sf. Filograninae). Recently it was found to occur in *Rhodopsis* (Ben-Eliahu & Ten Hove 1989) and in *Spiraserpula* as well (Pillai & Ten Hove, in

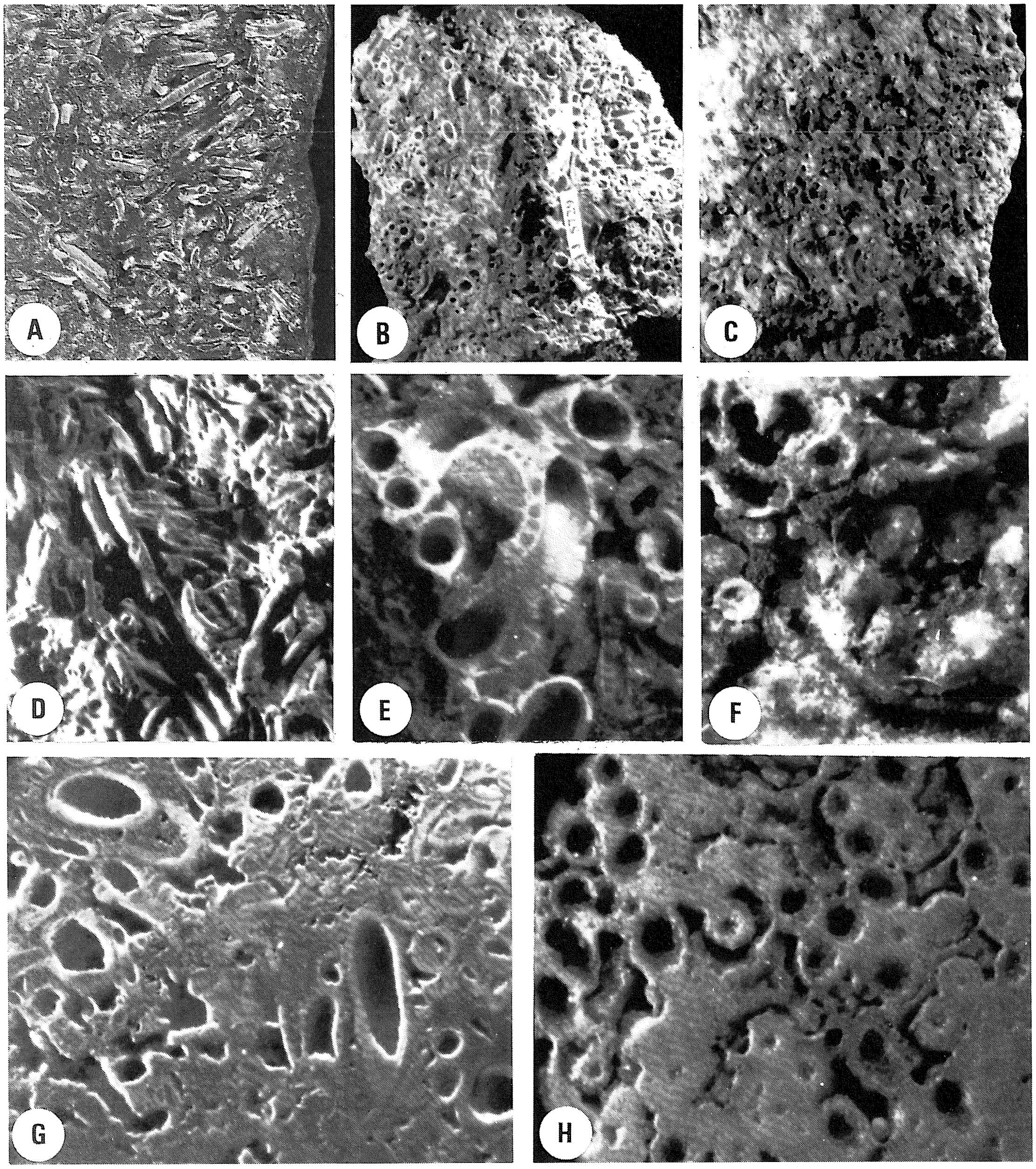

Fig. 7. Three serpulid limestones. A. Upper Jurassic Lower Serpulid Limestone consisting of *Serpula coacervata* mainly (Wöltjebuche, Deister Hills, Germany; ZMA V. Pol. 3754; 2.23 ×). Natural weathering has loosened the tube-fragments. B. Miocene (Spain, J5729; 0.88 ×). C. Pliocene (Spain, Pg 74 071; 0.88 ×). The difference between the natural growth position in the two Spanish pieces (7B, C) and the more or less oriented, redeposited fragments in the German limestone (7A) is evident. D–F. Details of Figs 7A–C respectively (all 3.7 ×). For close-up of Fig. 7D see Fig. 9C. Figures 7D–F again show the difference between accumulations of loose tube-fragments (D) and tubes clustered in growth position (E, F). G, H. Transverse cuts through specimens of Figs 7B, C (3.7 ×). Note difference in recrystallization between Figs 7E, G (Miocene) and 7F, H (Pliocene).

preparation). However, scissiparity is a slow process and cannot by itself be responsible for the up to 30 cm-large masses of *Filograna* (Fig. 1G). These masses were already figured by Dalyell (1853: pl. 34) and Bianchi (1981: pl. 1 fig. 5). *Filograna*'s tubes are small and fragile (diameter 0.2–0.35 mm, mean $x = 0.26$, Standard Deviation (SD) = 0.04; thickness of wall 0.015–0.03 mm, $x = 0.019$, SD = 0.005, n = 18; cf. Figs 1E, F). Representatives of the other genera are also small, with tube diameters of 0.2–0.5 mm (exceptionally 2 mm in *Spiraserpula*). Generally these taxa occur cryptically. Though they undoubtedly play a role as secondary frame builders, cementing rubble, it is unlikely that they will form major buildups.

2.4. Conclusion

In general, serpulid buildups are formed in unstable marine habitats, mostly mixo- or hyper-haline, by ecologically widely ranging species. At the periphery of their ecological ranges, aggregation is enhanced by a complex of environmental factors such as (avoidance of) predation and/or competition for food and space, and abiotic factors as salinity and temperature. Attributes of the animal itself: duration of the larval stage, habitat selection, gregariousness of larvae and conditioning of water by presence of congeners all contribute to aggregation.

Midlittoral belts of serpulids occur on semi-exposed coasts, whereas those of vermetid gastropods are developed best in exposed conditions. Real serpulid reefs occur sub- or infra-littorally, at 0.6–30 m depth, and mainly in sheltered lagoonal conditions. Their size and extent vary with local factors. The largest reef reported so far covers the walls of Ellis Fjord (Antarctica) over a length of more than 8 km, between 8 and 30 m depth, with an up to 1.5 m-thick layer of more or less erect, aggregated tubes.

Table 5. Simplified stratigraphy of Jurassic-Cretaceous boundary beds in NW Germany (after Casey et al. 1975).

Bückeberg Formation (='Wealden')	
Münder Formation	Serpulit Member (Upper Serpulid Limestone)
	Katzberg Member
	Münder Marl (with intercalated Lower Serpulid Limestone)

3. 'Upper Malm' serpulid limestones in NW Germany

3.1. Palaeogeographical setting

During the Late Jurassic, a large inland sea extended from the Netherlands-German border eastwards to Hannover (NW Germany), covering the area of the Lower Saxony Basin. The centre of this basin contains several hundred metres of 'Upper Malm' rock salt. Marls with intercalations of anhydrite and limestone occur below and above the salt as well as along the basin's margins (Brand & Hoffmann 1963, Betz et al. 1987). During the Early Cretaceous, limnic deposits of the Bückeberg Formation ('Wealden') were laid down in the basin.

Two levels of serpulid limestones have been distinguished in the Upper Malm: the Lower Serpulid Limestones (LSL), which are intercalated locally in the Münder Marl, and the Upper Serpulid Limestones (USL), which correspond to the so-called 'Serpulit' and which occur in places in the upper part of the Münder Formation, close to its contact with the Bückeberg Formation (Table 5).

The serpulid limestones outcropping to the southwest of Hannover and sampled for this study, have been dealt with in detail by Schönfeld (1979), who thoroughly investigated the Upper Malm in that area. The first author to describe these limestones, was Blumenbach (1803).

Serpulid limestones of similar age are known from Ochtrup and a few other places near the German-Netherlands border (Schott 1951; Kemper 1988), from central Poland (Kubiatowicz 1977) and from S England (Bazley et al. 1971, in Schönfeld 1979: 188).

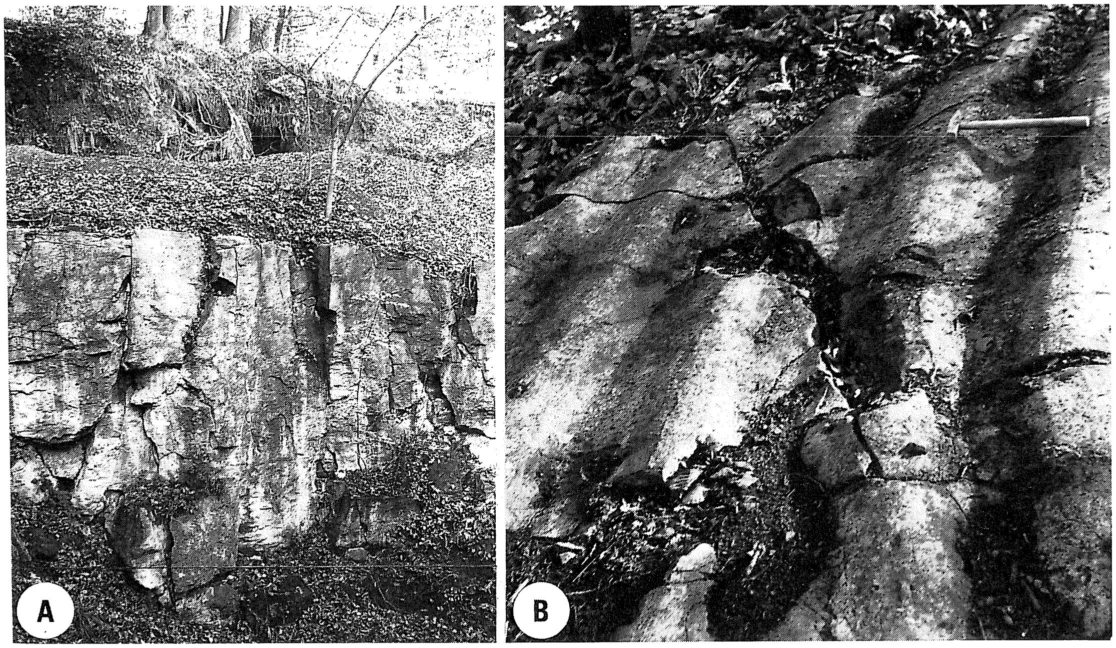

Fig. 8. A. Outcrop (about 5 m high) of massive Lower Serpulid Limestone (Wöltjebuche, Deister Hills, Germany; Upper Jurassic). B. Ripple-marks on top of same outcrop.

3.2. Localities studied, sample processing

The following locations were visited during summer 1983 to collect material of Jurassic-Cretaceous serpulid limestones:

NW Germany (locality nrs. are those of Schönfeld 1979: fig. 15): Hills of Deister.- S of Wennigsen, loc. 1, Wöltjebuche (Lower Serpulid Limestone, probable type locality of *Serpula coacervata*; ZMA V.Pol.3754) and loc. 37, 38, Hüttenweg and Lehmbrink (both Upper Serpulid Limestone)

- near Völksen, loc. 49, 50, 52, 72, Kalenberg and Lauseberg (Lower and Upper Serpulid limestones)

- S Nesselberg and NW Osterwald, loc. 105–108 (Upper Serpulid Limestone).

German-Netherlands border area: -NW of Ochtrup (E of Gronau), Mühlenberg (Jurassic; Kemper 1988: 14, 18). Small pieces of serpulid limestone were picked up from a corn field (ZMA V.Pol.3771). Outcrops could not be found; they are only known from ditches to build housing foundations.

- Lünten (Schott 1951). Only a small, fenced-in quarry filled with water could be found. Local people discouraged gathering material.

E Netherlands: Upper Jurassic serpulid limestones are mentioned from the eastern Netherlands in the Lexique Stratigraphique International (Europe 4aV), by Harsveldt (1977) and by NAM & RGD (1980). Cores from the boreholes concerned could not be retraced at the Geological Survey of the Netherlands in Haarlem. Core material from nearby localities (Schoonebeek 2, 760–796 m; Schoonebeek 3, 928–982 m, and Losser 3, ca 350 m) did not contain serpulid limestone.

The material was sawn and polished on several planes with carborundum powder up to coarseness 600. Efforts to make acetate-peelings failed because of the relatively soft consistency of the limestones. Since regular SEM pictures did not give enough information on the tube-wall structure, additional ones were taken from very fine-polished planes (1 μ), etched for 20 sec. with 30% citric acid. Measurements were taken under a stereo-microscope with an ocular micrometer.

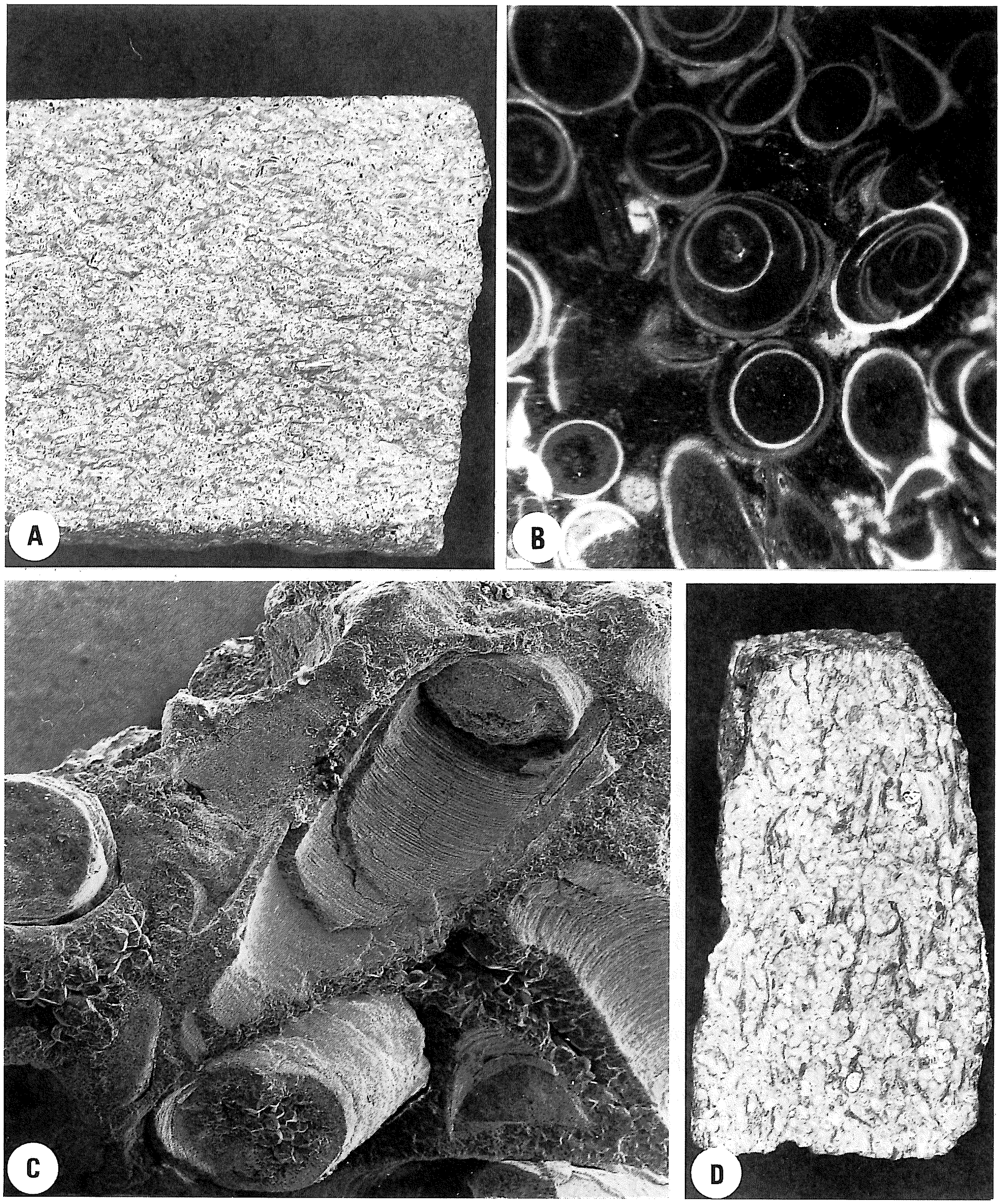

Fig. 9. A–C. *Serpula coacervata* (Wöltjebuche, Lower Serpulid Limestone; ZMA V. Pol. 3754). A. Tubes in calcareous matrix; vertical plane, sawn and polished (1.0 ×). B. Detail of Fig. 9A, showing telescoping of the tubes (30 ×). C. Scanning Electron Micrograph, close-up of part of Fig. 7A, showing transverse striation of outer tube-wall (43 ×). D. Serpulid limestone from Ochtrup, vertical plane, sawn and polished. Note bivalve fragments (E of Gronau, Germany; Jurassic; ZMA V. Pol. 3771; 1.4 ×).

3.3. Lower Serpulid Limestones

The LSL at Wöltjebuche are light to dark grey, and consist exclusively of the tubes of *Serpula coacervata* embedded in a calcareous matrix (Fig. 9A). They are 5 m thick and have well-defined contacts with under- and over-lying marl beds (Fig. 8A). The *Serpula* tubes are relatively small, max. 12 mm long and about 1 mm wide (Fig. 7A). They occur singly or in small clusters; sometimes smaller juvenile tubes are cemented to larger adult ones. Coiled juvenile tubes have not been observed. Most tubes are filled with smaller ones, up to five tubes telescoping into one another, or with tube grit (Fig. 9B). The tubes are oriented parallel to the bedding planes and to ripple-marks (Fig. 8B). The matrix consists of two micrites: one unstructured, the other pelletal-like. The latter is of biotic origin and resembles the micrite deposited by algae (probably the cyanophyte *Girvanella*) in the USL (Schönfeld 1979: 71, 111).

The LSL are very pure: 37–40% Ca and a maximum of 0.7% Mg. They do not contain detrital quartz, nor inclusions of sandy limestone, clay or marl. The proportion tubes versus matrix varies. The serpulid limestone facies in the area locally grades laterally and vertically into an oolite facies, or into a serpulid grit facies, containing 10–50% bivalve grit (M. Schönfeld, pers. comm.). It is hard to establish the lateral dimensions of the buildups; apparently they are relatively small, their thickness ranges from 1–6 m (Schönfeld 1979: 65–67).

The tubes were probably deposited in shallow water, in a relatively high-energy environment. As evidenced amongst others by the occurrence of horizons with flat pebbles ("Flachgerölle"), the marls between which the serpulid limestone is intercalated are definitely deposited in shallow-subtidal or intertidal environments (Schönfeld 1979: 75, 79, 82). The top of the limestone in places shows desiccation cracks.

The ambient salinities are ill known. Possible salinity-indicators as ostracods and bivalves are not present in the LSL (Gramann 1971). Serpulids themselves are unreliable indicators of salinity (section 1.3), although their mass-occurrences are mostly found under peripheral marine conditions (Ten Hove 1979b). For the LSL these most probably will have been either mixohaline or hyperhaline. The under- and overlying marl beds show indications of hyperhaline conditions like rock-salt, gypsum and celestite. On the other hand the strontium content of the serpulid limestone indicates a euhaline to mixohaline environment (Schönfeld 1979: 77–78). Jordan (1970: fig. 2) hypothesizes a general increase of the salinity in the entire inland sea during Münder Marl times, up to values between 40 and 160‰ near the basin borders.

3.4. Upper Serpulid Limestones

The USL (Figs 12A–E) are quite different from the LSL and consist of alternating serpulid limestones, stromatolites, stromatolitic-serpulid limestones, sandy limestones and marls. All biogenic components like serpulids, bivalves, ostracods and stromatolites are fragmented and worn, and form pronounced grit facies. The bivalves are heavily weathered by boring algae. The stromatolites are seldom found in the original growth positions, but generally as eroded pebbles and mostly in combination with serpulids. All these characteristics, together with the presence of many ooids and pellets, indicate a rather high-energy environment, probably peritidal. Locally, however, less fragmented layers of cyanophytes with a high micrite content are evidence of a more sheltered environment. The over- and underlying marls show evidence of mixomesohaline to limnic conditions, and include desiccation cracks (Schönfeld 1979: 105–109, 111, fig. 7).

The serpulid limestones from the German-Dutch border region (Ochtrup) were deposited disconformably on a Lias underground. Their stratigraphic position is not clear. In addition to these serpulid limestones (Fig. 9D), limestones mainly consisting of the bivalves *Neomiodon* and *Corbula* have been reported from the same locality (Kemper 1988). Stromatolitic algae occur as well (Schott 1951; from bore holes in the area).

It is not clear whether the Polish serpulid limestones mentioned by Kubiatowicz (1977) can be correlated to the German ones. Kölbel (1967) presents a map showing that the maximum basin extension at the time of the Münder Marl stretches throughout northern Germany towards Poland. However, it is questionable if there has been an open water contact. Serpulid limestones are not known from E Germany (formerly DDR; Kölbel 1967).

3.5. Systematic description

Phylum Annelida Lamarck, 1818
Class Polychaeta Grube, 1850
Family Serpulidae Rafinesque, 1815
Genus *Serpula* Linnaeus, 1758

Serpula coacervata Blumenbach, 1803 (Figs 7A, D; 8A–B; 9A–C; 10A–B)

1803 *Serpulites coacervatus* Blumenbach, p. 22–23, pl.2, fig. 8

1962 *Serpulites coacervatus* : Howell, p. W160, fig. 100–1 [copy from Blumenbach]

1979 *Serpulites coacervatus* : Lommerzheim, p. 140–141

1979 *Serpula coacervata* : Schönfeld, p. 65–66, figs 13, 43–45

1980 *Serpulites coacervatus* : Jahnke & Ritzkowski, p. 51, 59.

Original diagnosis: In the forest of Deister, near Wennigsen (west of Hannover), a thick, wide, distinct layer of solid limestone is found, entirely built up of very small serpulid tubes. The tubes are mostly milky white with a length of 1/24 foot and width of 1/20 inch. They are curved and have a circular cross-section. The outer surface of the tubes has a fine transverse striation. Although other serpulid species usually are attached to other fossils like belemnites or shells, these tubes are not connected to other fossils, but are all intertwined and cemented together, thus forming large beds (Blumenbach 1803; free translation; one Hannoverian inch was 24.4 mm).

Derivatio nominis: *coacervatus* means 'piled up', after the up to 6 metres-thick beds of this species.

Locus typicus: Deister Hills, W Germany, most probably the old quarry Wöltjebuche between Springe and Wennigsen (Schönfeld 1979: 66).

Stratum typicum: Münder Marl (Upper Jurassic), Lower Serpulid Limestone

Typus: Unknown to the present authors.

Description (based on topotypical material): Tube fragments are circular in cross-section, never flattened on one side, except for a small attachment area when fixed to another tube. The maximum external diameter is 1.1 mm; 35 cross-sections in a randomly chosen cm^2 had a range of 0.2–0.85 mm (x = 0.55, SD = 0.18). Most tube fragments are straight (Figs 7A, D); few are more or less curved. The length of the fragments is at most 12 mm. The tube-wall (Figs 9B, 10A, B) is very thin, 0.02–0.07 mm (x = 0.04, n = 18). The tube fragments show no signs of boring activities. Neither microscopic nor SEM observations gave much structural detail. The inside of the tube-wall is smooth; the outside shows very fine, transverse striae (Figs 9C, 10B). These striae are more or less irregular when observed under large magnification (> 100×), and alternatingly thicker and thinner. The density is about 50 striae per mm. There are no signs of peristomes nor fragments with a coarser or finer striation, indicative of a differentiated growth regime. Longitudinal keels, ridges or ribs are absent, as well as tabulae. Opercula are not known for this species.

Remarks: The generic name *Serpula* was emended by Blumenbach by adding *-ites* to the stem, solely to indicate that his species *coacervatus* was a fossil, without evidence that he proposed a new genus-group taxon. *Serpulites* therefore is a junior homonym of *Serpula* (*Intern. Code Zool. Nomencl.* art. 20). Little work has been done so far on the structure of the tube-wall in serpulids (section 1.4.1). Preliminary SEM observations indicate that the tube-wall of *S. coacervata* shows a uniform granular structure, unlike the multi-layered tube in e.g. *S. narconensis*. External tube-characters are virtually missing. In the absence of data, especially a comparative SEM study, the ichnotaxon *coacervata* can remain in the genus *Serpula*. It should be stressed, however, that it might be placed in other genera as well.

If the striation of the tubes were the result of diurnal activity, as in some corals, a life-span of 600 days for the 12 mm long fragments can be calculated from the number of approximately 50 striae per mil-

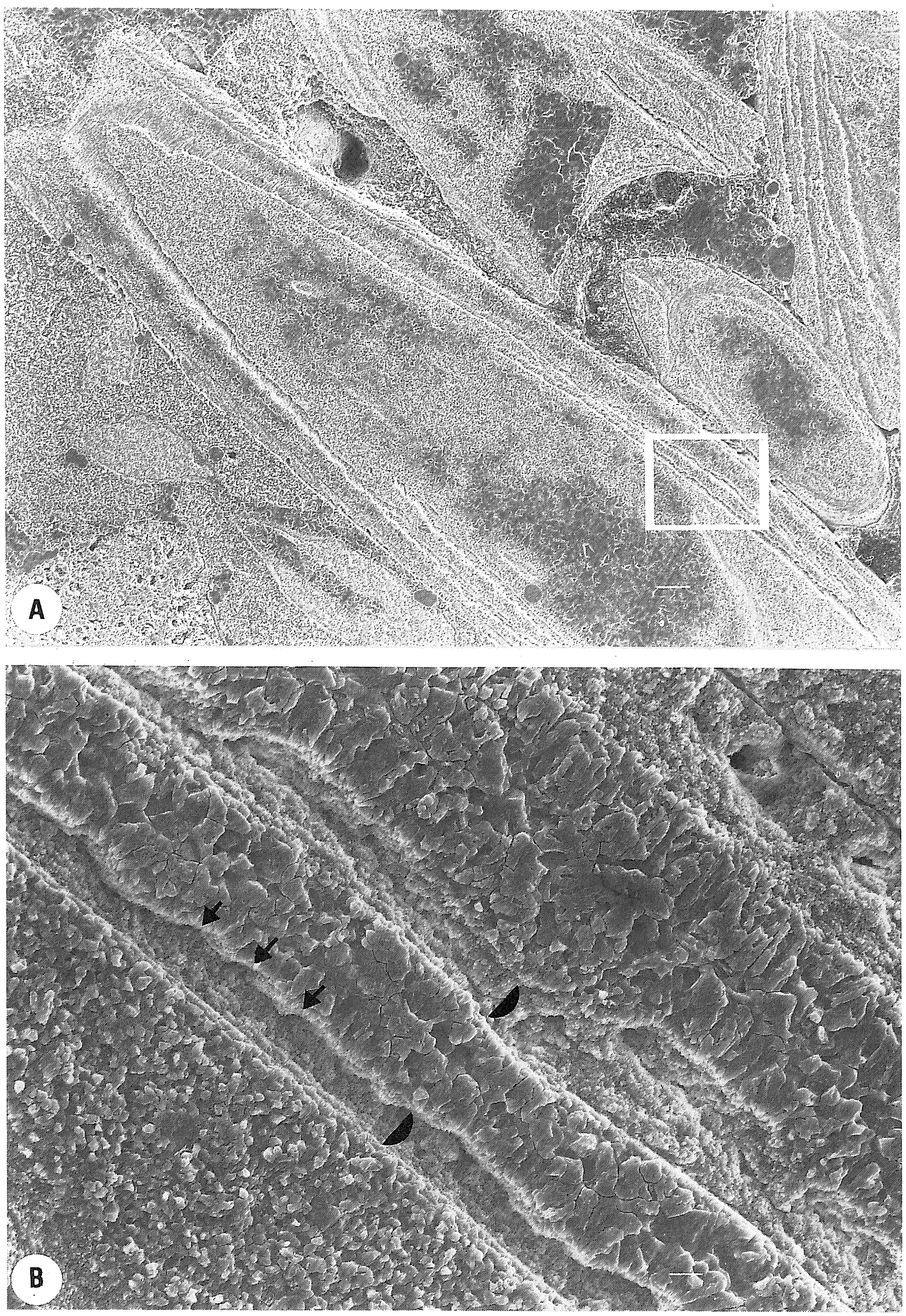

Fig. 10. A, B. *Serpula coacervata*, SEM of oblique longitudinal section of two telescoped tubes; sawn, polished and etched (locality as in Figs 9A–C). A. Scale is 0.1 mm. B. Enlargement of white rectangle of Fig. 10A; two tube-walls (indicated by half moons), both with smooth inner side and rippled outer side (cross-striations indicated by arrows; scale is 0.01 mm).

limetre. This would appear to be an unlikely low growth rate in view of the obviously good environment and the rates given in section 1.3.

Size and fragility of walls, absence of distinguishing characters as longitudinal keels or previous peristomes, are reminiscent of *Hydroides*, especially the Recent *H. elegans*, although the latter's average wall thickness (about 0.05 mm) and tube diameter (1.1–1.7 mm) are larger. This is one of the most common mass-occurring harbour-fouling species in the world. It is often misidentified as *H. norvegicus* or as *H. pectinatus* (Zibrowius 1971: 721–725). This similarity will have been the reason that Schmidt (1955: 46–47; section 3) used the name of the Recent *H. pectinatus* for the Miocene 'reef-forming' serpulid from Austria, which indeed is not unlike *Serpula coacervata*.

The material from Ochtrup is decidedly larger (Figs. 9D, 11), with a maximum external tube-diameter of 1.3 mm (in one randomly chosen cm^2: 0.4–1.1 mm, $x = 0.78$, SD = 0.16, n = 33) and a thickness of tube-walls of about 0.02–0.08 mm ($x = 0.05$, n = 10). Although identified as *S. coacervata* by Kemper (1988: 20), a close study is needed to confirm its identity.

Serpula coacervata is also reminiscent of *Serpulites* n. sp. Lommerzheim, 1979, from the Upper Cretaceous of Westphalia in western Germany. The longitudinal striation of the tube-wall in Serpulites n. sp. is a differentiating character.

Palaeoecology: The following tentative reconstruction of the palaeoenvironment is suggested, based on a comparison of the Lower and Upper Serpulid Limestones with other fossil and Recent examples. In addition, the environmental interpretation of the over- and underlying layers by Schönfeld (1979) was taken into account.

In both the Münder Marl (LSL) and the Serpulit Member (USL), the serpulid worm *Serpula coacervata* was forming reef fields on a muddy substrate in (a) large lagoon(s), fringing an inland sea. Fluctuating or permanently high or low salinities, the absence of competitors, and a more or less enclosed character of the lagoon(s) may have enhanced gregarious settlement of its larvae. The initial substrates for this settlement may have been shells or pieces of dead stromatolites. The increasing amount of tubes created new substrata for settling, thus enlarging the reef fields when reef heads fell apart. The fields were constantly eroded. Most tube fragments were selectively transported and deposited in monospecific banks of serpulid tubes (especially LSL). Other tube fragments were transported to places within the lagoon(s) where they became incorporated in living stromatolites, or served as initiating substrates for oncolites (USL).

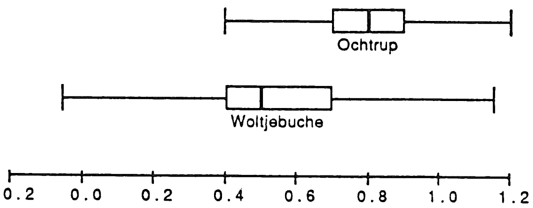

Fig. 11. Graphic comparison of tube-diameter (in mm) of *Serpula coacervata* from Wöltjebuche with material from Ochtrup. Boxes include 50% of the measurements; lines indicate entire range. Thick vertical lines are mean values. Full data can be found in section 3.5.

Unambiguous salinity indicators have not been found within the serpulid limestones. Over- and under-lying sediments indicate conditions fluctuating from hyperhaline to limnic, in shallow peritidal waters (Schönfeld 1979: 79, 109, fig.7; see also sections 3.6.2 and 4).

Geographic distribution: NW Germany and E Netherlands.

3.6. Discussion of palaeoecology

3.6.1. Historical

Blumenbach (1803), who originally described the species *Serpula coacervata*, did not explain the skeletal buildups. Credner (1863), Struckmann (1879), Koert (1898), Lerch (1913) and Schöndorf (1914a, b, c) only gave stratigraphic descriptions. Walther (1908, cited in Huckriede 1967) was the first to consider the limestones as remains of 'serpulid reefs', and compared these with the cup-reefs of the Bermudas (which, however, are algal-vermetid reefs: Ginsburg & Schroeder 1973). This opinion was followed by Haack (1909, cited in Huckriede 1967) and Dahlgrün (1923). Kauenhowen (1927) interpreted the serpulid limestones as fossilized accumulations of reef debris. Klingler (1955), unaware of the existence of Recent 'serpulid reefs', hypothesized that the tube-worms probably were living on floating algae, as do some Recent spirorbids. The limestone then would have been formed by accumulation of dead algae and tubes in shallow waters near the coast.

In the following years, Bischoff & Wolburg (1963) and Hoyer (1965) argued that there must have been a kind of a 'reef' or biostrome, because they observed no textural evidence for accumulation of floating epibionts. The weathered appearance of the tubes would be a result of in-situ reworking, implying a high-energy environment in shallow water. On the other side, Klingler was followed by Huckriede (1967). The latter stated that the tubes must have been growing on floating algae because the species never had been found growing on shells or stones (however, see section 3.6.2).

Schönfeld (1979) made a clear distinction between the Upper and Lower Serpulid Limestones. They are stratigraphically (Casey et al. 1975) and lithologically different. Other authors have been unaware of these differences, which at least in part will have added to the confusion. In Schönfeld's opinion the USL are a result of a stromatolite-serpulid co-occurrence. The LSL might be remains of such a co-occurrence as well, because the embedding matrix contains considerable numbers of cyanophytic pellets. High (wave?) energy would have been responsible for the in-situ destruction and reworking of the original growth form, which was probably an algal-serpulid 'reef'-field.

Jahnke & Ritzkowski described the facies sequence in the quarry of Thüste, south of Osterwald, where a 13 m-thick LSL is exposed, overlain by the same marly facies as in Deister. Applying Walther's rule of facies correlation (Middleton 1973; Woodford 1973), they concluded that the serpulid tubes have been reworked (from a non-specified original environment) and deposited along sandbars parallel to a stromatolitic reef (Jahnke & Ritzkowski 1980: fig. 3).

3.6.2. Comments

Lower Serpulid Limestones. Huckriede's argument that the serpulids were living on floating algae since the species never had been found growing on stones is moot for two reasons. Firstly, serpulids occurring on algae (common in spirorbids, rare in *Hydroides elegans*) have flattened attachment areas. The fragmented fossil tubes don't show attachment sides, except where they are attached laterally to each other. Moreover, it is unlikely that clusters of serpulids as occasionally found in the limestones could have survived on floating algae. Secondly, broken off free tube-parts of serpulid species in general are more or less circular, whilst the belonging adnate tube-parts can be triangular or trapezoidal. Free and adnate tube-parts often have not been recognized as belonging to one species.

Telescoping of tube fragments under the influence of wind and wave action, was observed by Reineck (1960) on the beach of the German island Norderney and by Bandel (1986: 41). Up to six tubes, pushed into each other, may be moving together and pile up, forming a bed of predominantly pectinariid tubes (Pectinariidae, Polychaeta; tubes of sand grains). This made Bandel explain the frequent occurrence of telescoped tubes in beds of the presumed annelid *Hyolithes kingi* Richter & Richter, 1941, from the Cambrian of Jordan. Applied to the LSL of Wöltjebuche, the telescoping, the weathered appearance, the parallel orientation of tube fragments and the ripple marks on top of the bed indicate a relatively high-energy environment.

There is little evidence for an in-situ reworked reef near Wöltjebuche. The limestone bank is monospecific. Bivalve species are present in an adjacent grit facies 100 m distant. This may point to differential sedimentation by selective transport.

A Recent example of selective transport is found on the Roggenplaat, a tidal flat in the Eastern Scheldt, SW Netherlands. It is inhabited by several bivalve and gastropod species like *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria*, *Mytilus edulis*, *Cerastoderma edule* and *Hydrobia ulvae*. Nevertheless, large monospecific banks of *Cerastoderma* shells occur on the northeast edges of the tidal flat (Bams 1987). Obviously the physical conditions like prevailing southwest winds, geomorphology, tidal currents and weight and structure of the shells are responsible for the accumulation of these banks. One of the few pointers to selective transport of Re-

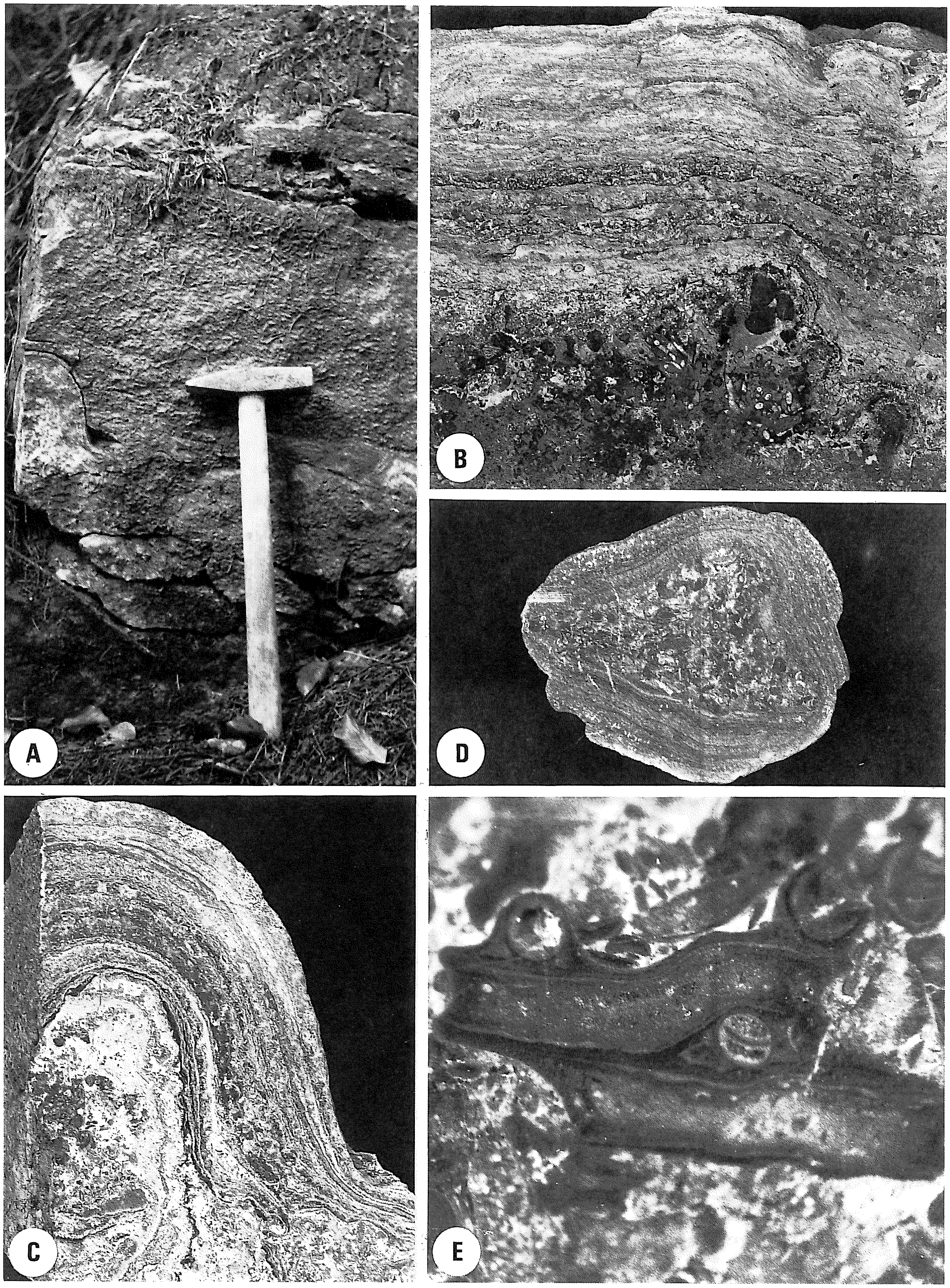

Fig. 12. Upper Serpulid Limestone. A–C. Lehmbrink (loc. 38 of Schönfeld 1979). A. Outcrop. B. Stromatolitic structure with a diffuse mass of serpulid tubes below, and alternating layers of algal growth (light grey) and serpulid tube-fragments (dark) above (1.45 ×). C. Stromatolite from left lower corner of Fig. 12A, vertical plane, sawn and polished. Note oncoidal nucleus around serpulid tube-fragments (0.65 ×). D, E. Osterwald (loc. 106 of Schönfeld 1979). D. Oncoid with nucleus of serpulid tube-fragments, and concentric stromatolitic layers (1.45 ×). E. Detail of nucleus; serpulid tube-fragments embedded in calcareous matrix (25.5 ×).

cent serpulid tubes may be found in the ambiguous statement by Saad (1974): "shell of dead bivalves, specially *Cardium* sp., and empty calcareous tubes of the serpliud (*sic*) worm *Mercierella enigmatica* accumulate nearly on the whole lake bottoms in great amounts. Some of these shells are transported by the action of wave and currents to the lake margin forming calcareous beds".

In-situ reworking at Wöltjebuche of a serpulid-stromatolitic growth form is also unlikely, because this should be visible as some kind of layering in the limestone bank. It is unlikely that erosion would destroy the stromatolite parts completely, and yet leave the fragile tubes in relatively good condition. Probably the tubes were supplied from elsewhere.

Upper Serpulid Limestones. Co-occurrence of serpulids ('vermetids' or 'spirorbids') and algal stromatolites, mentioned by several authors (Laporte 1967; Leeder 1973; Peryt 1974, 1975), suggests a biotic relation. In the USL most tubes occur in the centres of oncoids (Figs 12C, D) and in specific, well-separated layers towards the edges of stromatolites (Fig. 12B). Generally tubes are embedded separately in the matrix. Only few are cemented together in growth position; often they are broken (Fig. 12E). This implies that the serpulids in the centre of the stromatolites were dead before the algae started to form the oncoid or stromatolite.

Evidently, clusters of dead serpulids and calcareous mud were the initiating substrates for oncoid formation (Fig. 12D). When these oncoids became too heavy to be turned over, they developed into fixed stromatolites (Figs 12A, C). Serpulid tubes in the USL stromatolites are fragmented and only present in well-defined layers, together with pellets and other particles (Fig. 12B). Apparently the growth of the algal mats was regularly interrupted by sedimentation. Schönfeld (1979: 111, fig. 47) describes serpulids in growth position covered by stromatolites. His fig. 47 shows a fragment of a 20 cm-thick, 3 m-wide layer of serpulids, which in his opinion (pers. comm.) is evidence for a serpulid-stromatolite community.

Our conclusion is that there has been no other biotic relation between algae and serpulids than that caused by living in the same area. Clusters of dead serpulids were the initial substrate for the USL stromatolites, and algal mats incorporated empty tubes and other calcareous grains. Evidence for stromatolites providing a substrate for serpulid growth has not been found. It rather will have been the other way around. Serpulid reef fields probably were covered by stromatolites when conditions prevented further serpulid growth (as for instance in the centre of the Tunisian micro-atolls (section 2.2.2.3), during a prolonged period of higher salinity such as killed the reefs in Baffin Bay (section 2.2.2.2), or when excessive reef growth restricted water circulation in parts of the lagoon killing off serpulids).

This interpretation appears to be in concord with the 'spirorbid'-algal stromatolites (section 1.5.3), and with Recent stromatolites in a hyperhaline (55–70‰) lagoon near Shark Bay, W Australia. The colloform mat forming most subtidal stromatolites in that bay, is soft but coherent at the surface, and lithification of the structures begins a few millimetres or centimetres below, increasing progressively downwards (Playford & Cockbain 1976). It is unlikely that serpulid larvae (or spirorbids or vermetids) ever settle on this soft surface of living algae; they need a firm substrate. The lower parts of the stromatolitic columns are generally well lithified and commonly have a 'beard' of the chlorophyte algae *Acetabularia.* Masses of tiny serpulids encrust cavities in the sides of the stromatolites and they play a significant role in the construction of the margins (Playford & Cockbain 1976). The algal mats are growing on top of the columnar stromatolites, while the lower, lithified parts are not covered any more by living mats and serve as a substrate for epibiontic organisms, serpulids included. In contrast, the USL show small, rather diffuse stromatolites (Fig. 12A), which hardly have space for encrusting serpulids. Moreover, we did not find large clusters of serpulids in situ on these stromatolites, although aggregates of few serpulid tubes with stromatolites are not uncommon (M. Schönfeld, pers. comm.).

The Recent stromatolites in Shark Bay are constructed of sedimentary material, trapped and bound by algae, and cemented by aragonite. These solid structures are composed of about 80% angular shell fragments in the grain size range very fine sand to silt, and incorporate foraminiferal tests, small pelecypods, gastropods, worm tubes, pellets and detrital quartz grains (Logan 1961).

Recent stromatolite development in mixohaline inland lakes in the SW Netherlands starts from a wide variety of substrates: mainly bryozoan buildups of *Electra crustulenta*, but also from bottles, rubber tires and rush stems (Bijma & Boekschoten 1985). These lakes have relatively quiet waters, and few clastic sediment particles are incorporated in the stromatolitic layers, making them morphologically different from the USL stromatolites and the Recent stromatolites of Shark Bay. If the palaeoenvironment in NW Germany had been as quiet as in these mixohaline lakes, then the serpulid accretions probably would have been conserved by the stromatolites just as well as the fragile Recent bryozoan buildups. However, since we only found stromatolites with a nucleus of serpulid debris, the palaeoenvironment must have been more agitated.

4. Conclusions

At first glance the differences between the Recent serpulid reefs of Ardbear Lough in Ireland and the 'Upper Malm' buildups of NW Germany are striking. A great variety of (mainly mollusc) species lives on these Recent reefs, and contributes to the adjacent sediment. Such a diversity of accompanying species is typical for Recent serpulid buildups. Even those from extreme lagoonal environments, like Lake Tunis or Baffin Bay, are not monospecific, but contain associated species, just as the Mesozoic 'deep water' reefs. However, the serpulid limestones and adjacent grit facies of NW Germany contain very few non-serpulid species. This, and the local presence of stromatolites, indicates strenuous environmental conditions. Such conditions, notably widely fluctuating salinities and temperatures, are often a result of isolation, for instance in a more or less enclosed lagoon or fjord. Lack of circulation is one of the factors enhancing aggregating behaviour of planktonic larvae, like in serpulids. It may be inferred that the NW German buildups arose in lagoonal conditions, probably in lagoons fringing an inland sea. There is ample geological evidence for the existence of such a sea.

In the palaeoenvironment of Wöltjebuche no rock outcrops were present. However, many Recent and one Austrian Miocene example show that only a small hard substrate, even an oyster shell (Fig. 3D) or a piece of stromatolitic limestone, is needed to start a serpulid aggregate. Such small objects, no doubt, will have been present in the German palaeoenvironment as well. Once an aggregate has started to grow, dead fragments fall aside, and form new settling places. In this way even muddy substrates can be colonized by serpulids, and reefs may be formed.

The Recent Irish sediments contain large reef fragments, deposited near the source. The Mesozoic reefs from S Spain evidently have been preserved in situ. The fossil tubes from Wöltjebuche have a more fragmented appearance, apparently due to transportation. Probably originating from an 'open' meshwork (cf. Figs 1F, 4A, 5C) with spaced-out anterior tube-parts (as described for *S. vermicularis*, section 2.2.2.2), the thin and small fragments of *S. coacervata* are more liable to have been selectively transported than the fragments of the relatively solidly built Recent reef (cf. Fig. 4C). A grit facies, containing up to 50% bivalve fragments, only 100 m distant from the Münder Marl serpulid deposits, may be taken as further evidence for selective transport. The serpulid material may have accumulated in a depression in the lagoon, possibly a tidal channel.

The differences in tube deposition between the two serpulid limestones may be due to a lesser development of stromatolite-forming algae in the case of the LSL, and be related to slight changes in hydrology (M. Schönfeld, pers. comm.).

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Appendix

Annotated checklist of serpulid names.

Part of the confusion in the literature is due to mistaken identifications and erroneous nomenclature. For the clarity of this paper, we have replaced all erroneous names, as used in the papers cited, by their current names.

In this checklist, current names are given in *italics*, and with original author, year of publication, and original binomen. Synonyms, in regular lettertype, are cross-indexed.

Crucigera zygophora (Johnson, 1901), as Serpula zygophora
Ditrupa Berkeley, 1835
Ditrupa arietina (O. F. Müller, 1776), as Dentalium arietinum. Indo-Pacific records of this name belong to *D. gracillima*
Ditrupa crenata Ehlers, 1908, see *Serpula crenata*
Ditrupa gracillima Grube, 1878, pro parte synonymous: *D. arietina*
Ditrupa mosae (Bronn, 1837), see *Sclerostyla mosae*
Ficopomatus Southern, 1921, synonyms: Mercierella, Neopomatus
Ficopomatus enigmaticus (Fauvel, 1923), as Mercierella enigmatica. Palaeotropical records of this name belong to *F. uschakovi*
Ficopomatus uschakovi (Pillai, 1960), as Neopomatus uschakovi, p.p. syn.: M. enigmatica : Straughan 1972. In part her paper refers to *F enigmaticus* as well
Filipora filograna Dalyell, 1853, see *Filograna implexa*
Filograna Berkeley, 1835
Filograna implexa Berkeley, 1835, syn.: Filipora filograna
Filogranella elatensis Ben-Eliahu & Dafni, 1979
Filograna socialis (Goldfuss, 1831), as Serpula socialis, syn.: Sarcinella socialis
Filogranula Langerhans, 1884
Galeolaria Lamarck, 1818
Galeolaria caespitosa Lamarck, 1818, syn.: 'Serpula lithogena'
Helicosiphon biscoeensis Gravier, 1907
Hydroides Gunnerus, 1768
Hydroides dianthus (Verrill, 1873), as Serpula dianthus, syn.: H. hexagonus, p.p. syn.: H. uncinatus
Hydroides elegans (Haswell, 1883), as Eupomatus elegans. One of the most common harbour-fouling species of the world, temperate to tropical. Often erroneously mentioned as *H. norvegicus*, and as H. pectinatus
Hydroides hexagonus (Bosc, 1802), as Serpula hexagona, see *H. dianthus*
Hydroides norvegicus Gunnerus, 1768. An essentially boreal-lusitanian species. Records of this name from (sub)tropical harbours and lagoons generally should be attributed to *H. elegans*, for instance: Behrens 1968, Harbridge et al. 1976, Mastrangelo & Passeri 1975, Paul 1937, Vuillemin 1954a
Hydroides pectinatus (Philippi, 1844), as Eupomatus pectinatus. As mentioned by Hargitt 1912 and Schmidt 1955, see *H. elegans*; in part also see *H. norvegicus*
Hydroides uncinatus (Philippi, 1844), as Eupomatus uncinatus. Confused, complex of about 10 species. As used by Vuillemin 1954a, see *H. dianthus*
Josephella Caullery & Mesnil, 1896
Laminatubus Ten Hove & Zibrowius 1986
Marifugia cavatica Absolon & Hrabe, 1930
Mercierella Fauvel, 1923, see *Ficopomatus*
Mercierella enigmatica Fauvel, 1923, see *Ficopomatus enigmaticus*. However, palaeotropical records with this name generally belong to *F. uschakovi*; as used by Adamson & Pickard, see *S. narconensis*
Neovermilia Day 1961
Nogrobs Montfort, 1808, syn.: Tetraserpula
Placostegus Philippi 1844
Pomatoceros Philippi, 1844
Pomatoceros caeruleus (Schmarda, 1861), as Vermilia caerulea. Confused, New Zealand records see *Sp. cariniferus*
Pomatoceros coeruleus, error for caeruleus
Pomatoceros triqueter (Linnaeus, 1758), as Serpula triquetra. Often confused with the similar species *P. lamarckii* (Quatrefages, 1865)

Pomatoleios Pixell, 1913
Pomatoleios crosslandi Pixell, 1913, see *Pomatoleios kraussii*
Pomatoleios kraussii (Baird, 1865), syn.: Pomatoleios crosslandi
Protis Ehlers 1887
Protula tubularia (Montagu, 1803), as Serpula tubularia
Rhodopsis Bush, 1905
Sarcinella socialis (Goldfuss, 1831), see *Filograna socialis*
Sclerostyla Mörch, 1863
Sclerostyla mosae (Bronn, 1837), as Dentalium mosae, syn.: Ditrupa mosae
Serpula Linnaeus, 1758
Serpula *cf.* advena Salter, 1863, not serpulid but belonging to the Order Microconchida (see Weedon 1991)
Serpula coacervata Blumenbach, 1803, as Serpulites coacervatus
Serpula crenata (Ehlers, 1908), as Ditrupa crenata
Serpula (Cycloserpula) socialis Goldfuss, 1831, see *Filograna socialis*
Serpula helicalis Beus, 1980, not serpulid but belonging to the Order Microconchida (see Weedon 1991)
'Serpula lithogena' Péron & Freycinet, 1816, nomen nudum, most probably belongs to *Galeolaria caespitosa*
Serpula narconensis Baird, 1865, syn.: Mercierella enigmatica **non** Fauvel : Adamson & Pickard 1983.
?*Serpula octoforis* Dall, 1909, not serpulid but cirratulid polychaete *Dodecaceria fistulicola* Ehlers, 1901
'Serpula rectiformis' Clark, 1918, not serpulid but probably *Diplochaetetes mexicanus* Wilson, 1986, a *Dodecaceria*-like cirratulid polychaete
'Serpula saxistructuris' Howell & Mason, 1937, not serpulid but cirratulid polychaete *Dodecaceria fistulicola*
Serpula socialis Goldfuss, 1831, see *Filograna socialis*
Serpula vermicularis Linnaeus, 1767. Although reported worldwide, it is becoming increasingly clear that the name has been used for a complex of species. In this paper we have used the name in its restricted sense of an Atlantic-Mediterranean species only
Serpula zygophora Johnson, 1901, see *Crucigera zygophora*
Serpulites coacervatus Blumenbach, 1803, see *Serpula coacervata*
Spiraserpula Regenhardt, 1961
Spirobranchus Blainville, 1818
Spirobranchus cariniferus (Gray, 1843), as Vermetus cariniferus, partly syn.: Pomatoceros caeruleus
Spirobranchus polycerus (Schmarda, 1861), as Cymospira polycera
Tetraserpula Parsch, 1956, see *Nogrobs*
Vermiliopsis Saint-Joseph, 1894
Vermiliopsis pygidialis (Willey, 1905), as Vermilia pygidialis.

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