

share some antigens. In this regard, it is of interest that certain ultrastructural features of the trophozoites of *Sarcocystis* and *Toxoplasma* are similar (7).

The following characteristics of WC-1170 infection in mice are remarkably similar to those described for *S. muris* (3): (i) failure to transmit the parasite between mice by mouth, or parenterally, before 75 to 90 days after exposure, (ii) the finding of *Toxoplasma*-like cysts before sarcocysts are apparent, (iii) the appearance of morphologically typical sarcocysts some time between 40 to 60 days after exposure, but not before, (iv) absence of sarcocysts in the myocardium of infected mice, and (v) the morphologically distinctive trophozoite stage contained in the mature sarcocyst.

The *Toxoplasma*-like oocyst apparently initiated the sarcocyst stage in mice, although this was not definitely established. An alternative hypothesis is that we have been dealing with a mixed infection—an unusual strain of *Toxoplasma* shed in cat feces simultaneously with an unrecognized stage of *Sarcocystis*. This is unlikely since the *Toxoplasma*-like oocyst has been the only parasite found consistently in the feces of cats in transmission experiments. Furthermore, the experiments of Rommel *et al.* (8) and of Heydorn and Rommel (9), apparently demonstrating that an oocyst stage of *S. Tenella* and *S. Fusiformis* develop in carnivorous animals, supports the assumption that there is both an oocyst stage and a sarcocyst stage in the life cycle of the WC1170 parasite. Fayer's (10, 11) observations on cell cultures inoculated with organisms from sarcocysts found in the musculature of wild grackles suggested a coccidial type of life cycle for that parasite.

Since the discovery of *Sarcocystis* in mice 130 years ago, species of this parasite have been found in a variety of vertebrates including man. In spite of numerous investigations, however, the life cycle or cycles of *Sarcocystis* sp. have remained obscure. Of particular interest is the potential for human infection with the WC1170 parasite, which might ensue after exposure to cat feces, as appears to be the case with *Toxoplasma*. About 20 cases of human infection with *Sarcocystis* have been referred to (12), but some of these, in retrospect, were probably *Toxoplasma* infection (13). Human muscle is infrequently examined microscopically and most human infections have been an incidental postmortem finding. It is

also possible that man could become infected without the development of a typical sarcocyst, as apparently happens in some mice. In such cases, antibody to *Toxoplasma* might develop in low titer.

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Wood-Boring Bivalves, Opportunistic Species in the Deep Sea

Abstract. *Wood exposed for 104 days at a depth of 1830 meters at the permanent station of the research submersible D.S.R.V. Alvin was completely riddled by two species of bivalve wood borers (subfamily Xylophaginae, family Pholadidae). Their high reproductive rate, high population density, rapid growth, early maturity, and utilization of a transient habitat classify them as opportunistic species, the first recorded from the deep sea. Xylophaga is shown to be the most important species involved in decomposing woody plant material in the deep sea.*

During a dive of the D.S.R.V. *Alvin* (1) on 14 June 1972, panels of wood 36 by 16 by 2 cm were pushed 12 to 15 cm into the bottom sediment at a depth of 1830 m at the *Alvin* experimental site (39°46'N; 70°41'W), about 180 km south of Woods Hole, Massachusetts (Fig. 1). Two panels

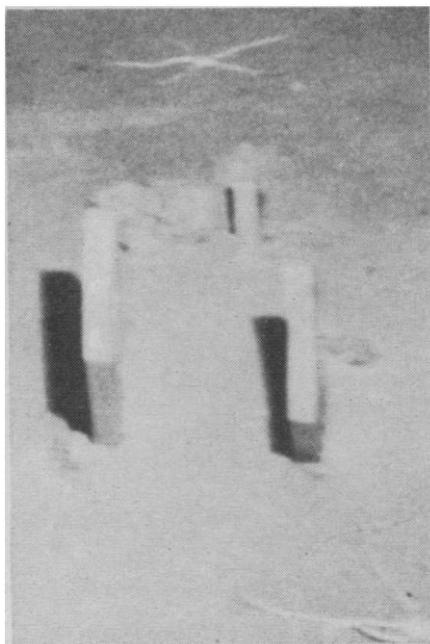


Fig. 1. Two pine panels in the bottom sediment at the *Alvin* station, at a depth of 1830 m.

were removed by the *Alvin* on 25 September 1972, after an exposure of 104 days. The wood was so weakened as a result of the activity of wood-boring bivalve mollusks (Xylophaginae, Pholadidae) that it began to fall apart while being picked up by the mechanical arm of the *Alvin* (Fig. 2). The minute openings of their burrows covered the surface, averaging about 150 per square centimeter (Fig. 2b), and in some areas the surface had fragmented and broken away (Fig. 2c). The boring bivalves penetrated from both sides, meeting in the middle (Fig. 3), and the burrows of the largest specimens were about 20 mm in length. These specimens were stunted (2) because their growth was limited by the lack of space, but the gonads were nearly ripe. Removal of all specimens from a 3-cm² section showed that two species were present, *Xylophaga* n. sp. and *Xyloredo ingolfia* Turner, in a ratio of about 5 to 1. The larval shell of the latter is brown and that of the former is white, so the two species can be readily separated at a very young stage. Both species were represented by newly attached or recently metamorphosed specimens as well as specimens which had penetrated the wood to a depth of over 5 mm, which indicated two settlements for each. Examination

Table 1. Groups, other than Xylophagainae, containing deep-sea species that utilize terrestrial plant material.

| Group | Association |
|-----------------------------|--|
| Mollusca | |
| <i>Idasola</i> (24, 25) | Byssally attached |
| <i>Myrina</i> (25, 26) | |
| <i>Chitons</i> (27, 28) | |
| Patelliform gastropods (28) | On surface, in borer tubes |
| Echinodermata | |
| <i>Hygrosoma</i> (20) | Feeds on terrestrial plant material |
| <i>Hapalosoma</i> (20) | |
| <i>Aroosoma</i> (20) | |
| <i>Pygmaeocidarus</i> (20) | |
| <i>Micropyga</i> (20) | |
| <i>Plesiadiadema</i> (20) | |
| Crustacea | |
| <i>Onesimoides</i> (29) | Feeds on terrestrial plant material |
| <i>Bathyceradocus</i> (29) | |
| <i>Melita</i> (29) | |
| <i>Xylopagurus</i> (30) | |
| <i>Janira</i> (31) | Lives in hollow stems Lives in wood |
| Annelida | |
| Polychaetes (28, 32) | In crevices and borer burrows |
| Sipunculida (28, 33) | In wood |

of the gut showed that both species have a large, full wood-storing cecum and so, like other Xylaphagainae (3, 4), they undoubtedly utilize wood for food. In addition to the Xylophagainae, numerous specimens of *Idasola argentea* (Jeffreys), a species of small deep-sea bivalve (family Mytilidae), were found attached by byssus threads to the surface, in crevices and in empty *Xylophaga* burrows. The rate and extent of this attack was surprising; wood

used in earlier experiments made in the Tongue of the Ocean, Bahama Islands, and off San Miguel Island, California, at similar depths and with exposures of 6 months to 3 years, although riddled, had not begun to crumble (5, 6).

The geographical distribution of the Xylophagainae is dependent on the presence of wood, and their dispersal on the free-swimming larval stage. Once the larvae have settled and metamorphosed into the adult form they are

incapable of moving to another piece of wood, and if the wood disintegrates they die. At the time the panels were implanted by the *Alvin* no wood was observed in the immediate area, although wood has been dredged in the general vicinity. Reflecting on the proximity of wood and the source of the larvae responsible for the attack, one can hypothesize that: (i) the adult borers have the ability to detect the arrival of new wood from a considerable distance and are thus triggered to spawn (this hypothesis is unlikely); (ii) the larvae have the ability to delay metamorphosis, and to detect wood at a considerable distance and actively swim toward it; or (iii) the larvae are produced in great abundance, are carried by bottom currents, have the ability to delay metamorphosis, and settle when chance encounter brings them in contact with wood.

Typically, the heaviest settlement of *Xylophaga* larvae occurs in the first 20 cm above the sea-sediment interface (5-7), and this was evident on the panels set by the *Alvin* (Fig. 2b), the number settling decreasing slightly toward the upper end of the panels. If the larvae can delay metamorphosis and remain in the plankton for long periods of time, one would expect to find them in plankton tows made near the bottom at any time of year, particularly in an area of heavy attack. However, none were found in bottom tows made at the *Alvin* site in June 1972 (8). A search will be made of subsequent tows when these become available for study. The small size of the borers (9) in the wood and the presence of newly settled larvae suggest an August settlement. Reproductive periodicity in the deep sea has been postulated for isopods (10) and ophiuroids (11), but it is considered atypical because the "monotonously constant conditions of the deep sea provide no seasonal pulses" (12). The complete lack of *Xylophaga* larvae in the plankton tows made in June, in contrast to the extremely heavy set on the panels, suggests cyclic reproduction. A working hypothesis and one to be investigated is that the breeding season of the Xylophagainae, and possibly other invertebrates dependent on terrestrial plant material for food or substrate (Table 1), may be tied to the rainy season in the tropics and the spring runoff in high latitudes. At such times large amounts of wood are flushed into the sea (13). A late summer spawning off the New England coast would allow time for wood,

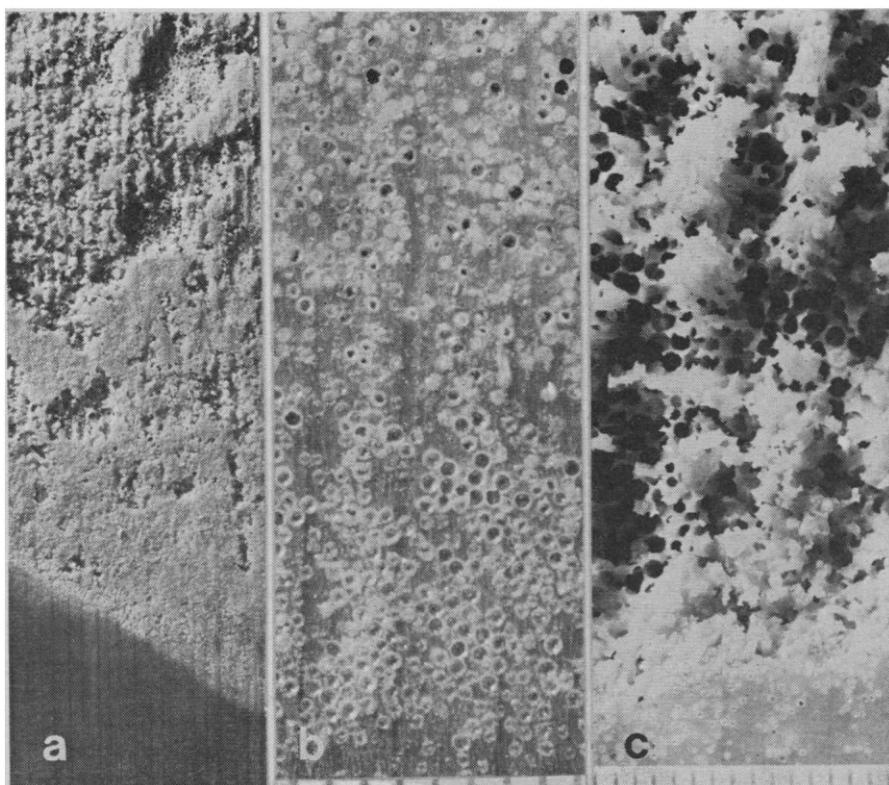


Fig. 2. (a) Section of a panel showing the mud line and extent of attack. (b) Close-up of the surface showing the burrow entrances; the large black holes are empty tubes of dead specimens. (c) Close-up of a section where the surface has disintegrated. (The scales are marked in millimeters.)

reaching the sea during spring freshets, to be carried well offshore, become waterlogged, and sink to the bottom

According to Jannasch *et al.* (14) microbial decomposers, other than those which may occur in the gut of invertebrates (15), exhibit little activity at great depths, and Kohlmeyer (16) reports the same for fungi. The Xylophagainae utilize wood both as a substrate and for food (either as host organisms for symbiotic bacteria in the gut or by means of an endogenous cellulase). It is now apparent that they are the most important deep-sea organisms involved in converting woody plant material to available food sources (i) in the form of fecal pellets for detritus feeders, (ii) as larvae or adults, exposed by the disintegration of the wood, for predators, and (iii) as dead remains for scavengers.

High population densities, high reproductive rates (17), early maturity, rapid growth, apparent ease of dispersal, and the ability to utilize a transient habitat make these wood borers classic examples of opportunistic species (18), the first recorded for the deep sea.

It has been noted that dredge hauls rich in terrestrial plant material also contain a great variety of animals (19–21), indicating that a patchy, uneven distribution develops around islands of such material. Wood carried far out to sea and sinking at scattered points is relatively transient and favors opportunistic species. In deep water off the mouths of rivers, off swampy or wooded coastlines, and in trenches, wood is a more common feature of the bottom (21) and produces a continuing patchy environment. These more persistent but constantly shifting "islands" allow for the development of opportunistic species, serve as dispersal centers from which larvae emanate to settle on isolated islands, and contribute to habitat diversity, niche specialization, and enrichment.

The arrival of wood on the bottom may be thought of as a "predictable disturbance" in the sense of Dayton and Hessler (22), the role of the borers as decomposers of the wood being comparable to that of the "croppers" in utilizing and distributing the animal remains. The predictability of the arrival of wood on the bottom allowed for the evolution of the Xylophagainae, while the unpredictability of the point of arrival led to their opportunism. Such disturbances do not detract from the stability-time hypothesis proposed by Sanders (23) to explain diversity in the deep sea. Rather, they add factors



Fig. 3. Section through the panel in Fig. 2, showing burrows entering from both sides, the specimens meeting in the middle. (The scale is marked in millimeters.)

contributing to diversity without altering the present view of the abyss as a predictable environment.

The validity of these ideas can be tested by (i) analyzing the effects of introducing islands of woody plant material and (ii) dredging and submersible programs designed to look at the quantity and distribution of land plant material in the deep sea in conjunction with a study of river effluents and ocean currents.

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Succession: Similarities of Species Turnover Rates

Abstract. *The rate coefficients for species turnover (the proportion of species lost per unit time) for successional communities decrease as the communities approach some equilibrium state. This observation makes it possible to determine the parameters of a two-parameter model which quantifies the time variation of successional changes in the second derivative.*

Several investigators (1) have noted common features of ecological succession (the orderly progression of ecological communities through time); for example, species diversity, structural complexity, biomass, and perhaps sta-

bility commonly tend to increase with the successional age (time since perturbation) of an ecosystem. We examined the rate coefficients for species turnover in published studies on succession (2) to associate community dynamics