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Flatworms Afloat

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*D. nitidus* subzone. Thus, initial destruction of this ancient continental margin can be dated with considerable precision. Detailed stratigraphic implications of this will be published elsewhere.

Distinctive conodonts are also restricted to extremely shallow water environments. A prime example is provided by the neurodont (fibrous, hyaline) conodonts of the Middle Ordovician. They form a littoral community found in intertidal and lagoonal carbonate environments which probably experienced both high temperatures and salinities<sup>2</sup>. Their virtual absence in deeper shelf facies also suggests a benthic habit<sup>19</sup>. Higher energy environments, developed as local shoal banks or around monadnock islands are characterised by more massive, robust elements. The niches occupied by these neurodonts were largely destroyed with the complete submergence of the North American craton during the late Ordovician, thus explaining their extinction.

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## Flatworms afloat

ON March 1, 1975 we sighted from the air, on the surface of the sea near La Paz, Baja California (Mexico), some unusual reddish brown streaks, extending for several hundred metres obliquely to the shore. On the following day we relocated them by ship (RV Dolphin) and found them to consist of high densities of the dinoflagellate *Noctiluca* and of a polyclad turbellarian, provisionally identified as *Stylochoplana sargassicola* (Mertens). Although blooms of *Noctiluca* are not uncommon<sup>1</sup>, marine pleustonic flatworms in large numbers are virtually unknown.

Between March 2 and 10, 1975 we made about 20 neuston tows across an area between 22°N and 25°N, and between the western coast of the Baja California peninsula and 110°W. We used a neuston net with fine nylon mesh cod end (202 µm pore size) supported by floats, and sampled swaths of the ocean surface 1 m wide (mean depth 10 cm, depending on wave size) and several hundred metres long. Samples from the brown patches in the La Paz harbour area proved to consist largely of *Noctiluca*, with an admixture of other dinoflagellates; it is probable that the latter were responsible for the brown colour, but that we collected relatively few of them because they were of a size to pass through the pores of the net. We were surprised that samples from all the other brown patches sampled on subsequent days consisted almost exclusively of brown flatworms, associated with more typical pleuston organisms<sup>2</sup> such

as *Porpita*, *Physalia*, *Glaucus*, *Ianthina*, *Pleurobrachia*, various smaller copepods, amphipods, decapod megalopa and fish larvae, and, in some tows, an abundance of terrestrial insects. The flatworms were especially numerous in tows taken between 24°20'N and 23°50'N, in some cases clogging the net. A rough calculation indicated that in one area, sampled on March 8, 1975, the surface density of these worms reached 1 m<sup>-2</sup>. They decreased markedly in abundance south of this zone, and were absent altogether from samples taken south of 23°N.

The animals, of all sizes from 2 to 12 mm long, were beautifully camouflaged among the leaflets of the brown alga, *Sargassum* sp., with which they were often associated. Since the green or brown colorations of certain marine turbellarians, notably species of *Convoluta*, are attributable to the presence of symbiotic algae (respectively, *Platymonas* and *Licmophora* spp.<sup>3,4</sup>), we suspected that the brown granules which constituted the speckles in the body wall of our worms might be symbiotic diatoms or dinoflagellates. They were, however, much too small, too dense and too irregular in shape, and we concluded that they were granules of animal pigment. Unlike dinoflagellates (or *Sargassum*), they did not turn green when denatured by boiling, drying or freezing, and did not yield a green solution when the animals were extracted with acetone, so we dismissed the possibility that they were, or contained, chloroplasts.

The animals displayed three quite distinct modes of movement. (1) They could glide (a few mm s<sup>-1</sup>), presumably by ciliary movement, on solid substrates (such as seaweed, fish or ctenophores) or on a relatively undisturbed air-water interface. (2) They could swim slowly, in a horizontal position, by undulations of the lateral margins of the anterior two-thirds of the body. (3) Alternatively they could progress much more rapidly by turning on one side and swimming, like a tadpole or small fish, with serpentine undulations, one or two per body length. This mode of progress was presumably noted for *Planaria pellucida* by Mertens<sup>5</sup>, who described it as "geschlaengelt" and likened it to the swimming movement of polychaete worms.

They readily settled on most solid substrates (weed, net, bucket and so on) from which they could be dislodged only with difficulty. (They seemed to prefer not to settle on *Porpita*, being perhaps repelled by its stinging nematocysts.) Specimens were rarely observed to be attached by only the posterior end, while the rest of the body swayed freely in the water. They were not seen feeding.

Clusters (3-6 mm diameter) consisting of hundreds of white eggs (100 µm diameter), which may have been laid by these worms, were found attached to the surface of *Sargassum* thalli collected in the same tows. They contained embryos, consisting of a few cells, or early blastulae; their further development was not observed.

Although many marine littoral turbellarians have been described, there have been few reports of truly pelagic species. Hyman<sup>6</sup> mentioned none in her review of marine turbellarians of the Pacific coast of North America. We have been able to trace in the literature several records of pelagic flatworms, but their taxonomy seems to be rather confused. Our specimens closely resemble the polyclad flatworm *Stylochoplana sargassicola* (Mertens)<sup>7</sup> described from the Sargasso Sea by Mertens<sup>5</sup>, who found it associated with the seaweed, *Sargassum bacciferum*. It is cryptically coloured, being translucent and speckled with pale yellow or yellowish grey pigment granules. This worm is not confined to the Sargasso Sea, however; it has been found elsewhere in the Atlantic Ocean between 21-35°N and 36-38°W. This species may be synonymous with *Stylochus pelagicus*, described by Mosely<sup>8</sup> from specimens collected along with *Halobates* and other pelagic animals off the coast of Sierra Leone. On both occasions when this worm was collected (August 1873, between 9°21'N 18°25'W and 5°48'N 14°20'W) the sea was highly phosphorescent, presumably, as in our own case, due to large numbers of dinoflagellates such as *Noctiluca*. Apparently *S. sargassicola* has never been reported from the Pacific Ocean before.

Von Graff<sup>7</sup>, who referred the nine described pelagic turbellarians to three species (and who also described two new species), recorded another flatworm, *Planaria pellucida* Martens, from the Atlantic as well as the Pacific Ocean. This species, originally described as *P. oceanica* by Charles Darwin<sup>8</sup>, was found about 150 miles from Natal, Brazil (5°S 33°W) in February, 1844. Mertens<sup>5</sup> collected his specimens about 500 miles offshore at 7°48'N 23°56'W, where they occurred together with typical pleustonic organisms such as *Porpita*, *Glaucus* and *Physalia*. This species is also somewhat transparent, but the body is whitish yellow, without evident spots. Our specimens seem to be morphologically quite different from *P. pellucida*.

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## Production of threitol and sorbitol by an adult insect: association with freezing tolerance

WE report here that in adult tenebrionid beetles, *Upis ceramboides*, an unusual combination of two polyhydric alcohols, sorbitol and threitol, is associated with the ability to tolerate prolonged freezing to at least  $-50^{\circ}\text{C}$ . The occurrence of threitol is of particular interest, since this compound has not previously been found in nature<sup>1</sup>.

Following the discovery that immature insects may produce glycerol during diapause<sup>2</sup>, polyhydric alcohols, usually glycerol, have been implicated as cryoprotective agents in a variety of overwintering insects<sup>3,4</sup>. Because of its relatively small molecular size, glycerol is able to penetrate most cell membranes, and its ability to prevent freezing damage is generally believed to lie in its colligative properties and its ability to act as a solvent, keeping potentially harmful salts in solution as they are concentrated during ice formation<sup>5</sup>.

Although non-penetrating compounds, including sorbitol and mannitol, are reported to have cryoprotective action on isolated cells<sup>5</sup> there are no reports of such a function in whole insects. Sorbitol has been found in the eggs of two insects<sup>6,7</sup> and in the larva of the dipteran *Eurosta solidagenis*<sup>8</sup>. The latter insect is tolerant to freezing but the function of sorbitol is obscured because glycerol is also present. The only other polyol reported to occur in insects is mannitol, which occurs with glycerol in the eggs of the overwintering aphid *Hyalopterus*<sup>9</sup>.

Freezing tolerance in an adult insect was first documented in a carabid beetle, *Pterostichus breviocornis*<sup>10</sup>, and is associated with the accumulation of large quantities of glycerol<sup>11</sup>. A more extensive survey of overwintering northern insects has revealed a number of freeze-tolerant species (L. K. M., unpublished), but *Upis ceramboides* is of particular interest because its large size ( $\sim 150$  mg) makes analysis of a variety of haemolymph constituents in each individual possible. It overwinters in a very exposed habitat above the snowline, and, as we show here, synthesises large quantities of polyols other than glycerol.

Adult *Upis* may be found throughout the year in interior Alaska and Canada beneath loose bark of aspen, birch, and spruce. During winter, air temperatures in these regions may fall to  $-50^{\circ}\text{C}$  and they often remain below freezing point for many months. Beetles collected during winter and brought into the warm laboratory recover their normal locomotion and frequently begin to feed within several hours. The relative scarcity of *Upis* has made it necessary to accumulate data over a 4-yr period to obtain sufficient seasonal information. In addition to analysis of haemolymph polyols, information was obtained on lower lethal temperatures, supercooling points and other physicochemical characteristics not included here. Because of the temperature lability of insect polyol levels, care was taken to perform all tests less than 1–2 h after specimens were brought into the laboratory. If specimens had to be stored, they were kept outdoors in conditions approximating natural ones.

Supercooling points have been determined using a thermoelectric technique on a large number of specimens and average  $-6.3^{\circ}\text{C}$ , which is quite high for a cold hardy insect and, surprisingly, shows no significant seasonal variation in spite of changing polyol levels. Initial tests for polyhydric alcohols using paper chromatography with several solvent systems showed that no glycerol was present but that sizeable amounts of either sorbitol or mannitol, and what was believed to be erythritol, were present during the winter months. Polyol levels drop to undetectable amounts in the summer and build up during the autumn (Fig. 1).

To identify whether it was sorbitol or mannitol that was

**Fig. 1** Haemolymph concentrations of threitol (---, ○) and sorbitol (—, ●) during the year and their relationship with lower lethal temperatures in *Upis ceramboides*. Data points represent individual values obtained over a 4-yr period from 1970–71 to 1973–74. Polyol levels were determined using paper chromatography with a solvent system of butanol–acetic acid–water (12:3:5 v/v), and periodate followed by borate–starch for detection. Positive identification was by GLC using a 150 cm  $\times$  3 mm glass column with 10% SP-2401 on Supelcoport 100/120, 220  $^{\circ}\text{C}$  column temperature. Lower lethal temperatures represent 100% mortality following a 1-h exposure to the final temperature. Cooling rates were  $0.3^{\circ}\text{C min}^{-1}$ .

