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THE LIFE CYCLE OF ASELOMARIS MICHAELI, A NEW GYMNOBLASTIC HYDROID

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The following account is of a hydroid not previously recorded, from the Atlantic coast of North America. It appears to be a form related to *Rhizorhagium* as redefined by Rees (1938), though not close enough to be included in that genus without a broadening of the definition and a reconsideration of the genera *Garveia* and *Bimeria*. Its closest relative appears to be *Atractylis arenosa* Alder (1862). According to Totton (1930), however, *Atractylis* is sunk in the synonymy of *Bougainvillia*, and *A. arenosa* is in any case in need of a new generic name. It is therefore proposed that the *Atractylis arenosa* of Alder become *Aselomaris arenosa*, and that the hydroid described here, which lacks the striking pseudohydrotheca and gelatinous perisarc of *A. arenosa*, be known as *Aselomaris michaeli*. This is in accordance with the views expressed by Rees and Totton (in personal correspondence). The genus *Aselomaris* is consequently defined as follows: bougainvillid hydroids with hydranths arisng singly from creeping stolons, with gonophores reduced to sporosacs and arising from the hydranth stalk, not from the stolons.

The present species was found throughout the general region of Boothbay Harbor, Maine, attached to the sides of floats, occasionally on Fucus fronds, in widely separated localities, namely, Lobster Cove, Townsend Gut, and the Town wharves. In every place it was associated with *Bougainvillia superciliaris* which it resembles in some respects, such as color, size and form of the hydranths.

Concerning its distribution, either it is an extremely local species or it has been extensively overlooked elsewhere. While a shallow water form, it is undoubtedly most inconspicuous. At the same time it should have been found if it occurred in the intensively collected Woods Hole region. Collections to the north have been more sporadic and its presence is therefore in doubt. It is quite possible that this is a northern species extending down to but not south of Cape Cod.

Aselomaris michaeli

This hydroid forms an encrusting mat often several centimetres square but with very little height. In fact most of the specimens obtained were collected only by shaving off the wood to which they were attached. The general nature of the hydranths is shown in Figure 1A. The hydranth grows vertically from the creeping stolon, the perisarc stopping short just above the base of the hydranth proper. It

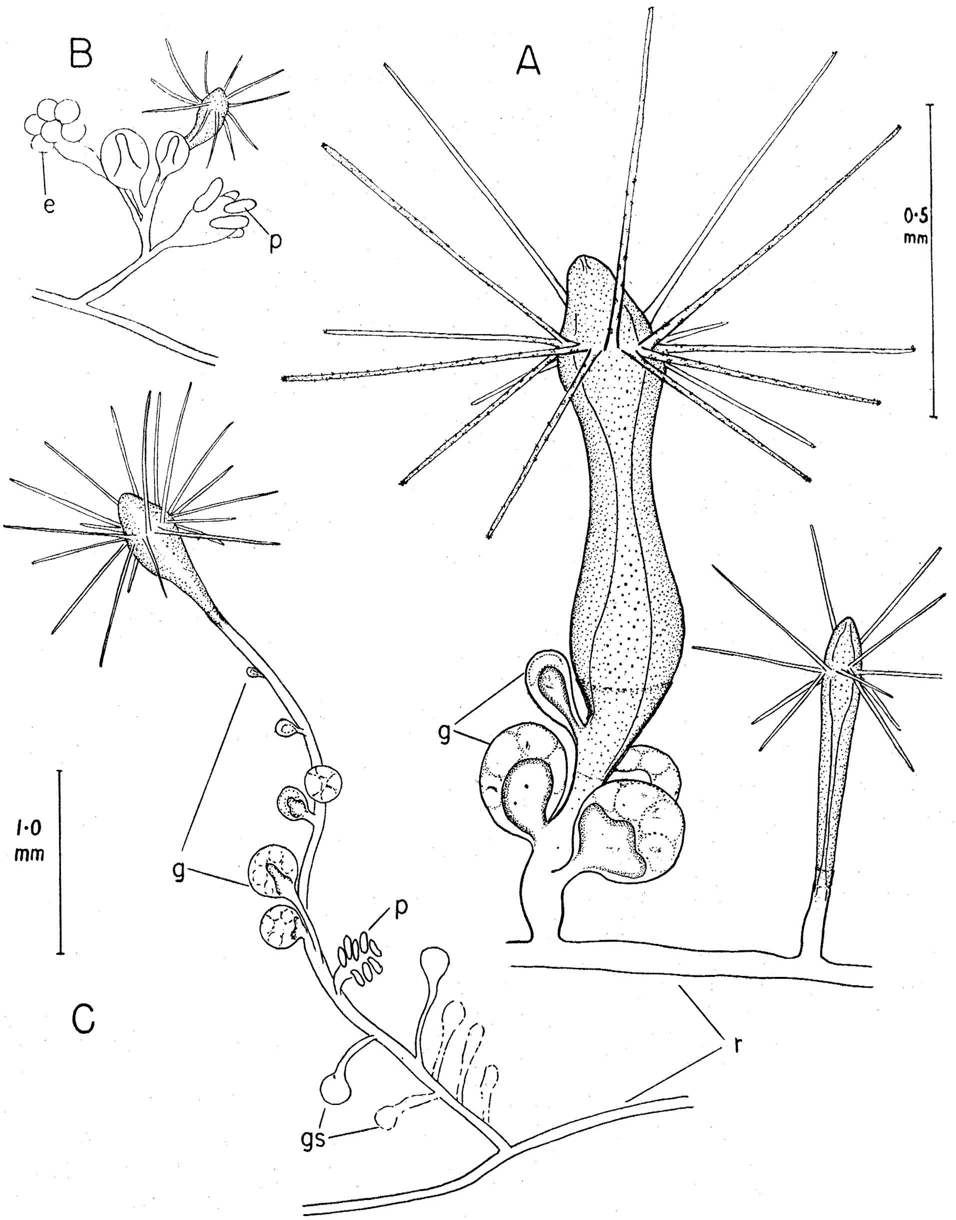

FIGURE 1. *Aselomaris michaeli.* A, large and small hydranths arising from the creeping hydrorhiza. B, somewhat older hydranth, at reduced scale, showing developing gonophores, gonophore with developing eggs and gonophore with planulae. C, maximum length hydranth, at same scale as B, showing succession of gonophores from distal juveniles to proximal stalk remnants. e, eggs; g, gonophore; gs, old gonophore stalk; p, planula; r, hydrorhiza.

has the form typical of the Bougainvillidae, with a conical manubrium and a single whorl of filiform tentacles. The tentacles are characteristically directed distally, laterally and proximally with virtually the same number in each category (Fig. 1A).

New hydranths grow only from the creeping stolon. Gonophore buds grow laterally from the base of the hydranth immediately proximal to the junction of naked and perisarc-covered coenosarc. This is a region of growth in a double sense. Not only are gonophores initiated, but the hydranth stalk grows in length, in effect pushing the growing gonophores down the stalk; that is, the new stalk that is progressively added proximally secretes chitinous perisarc and carries with it the growing gonophore, while new material and new gonophores are successively added between the first formed gonophore and the hydranth base. Thus we get a continually lengthening stalk bearing a series of gonophores, youngest nearest the base of the hydranth and oldest near the junction of the stalk and hydrorhiza (Fig. 1C).

No branches are given off and the hydrorhiza forms a closely applied creeping stolon. The only outgrowths are the buds arising from the hydrorhiza that develop directly into hydranths; that is, gonophores do not develop directly from the hydrorhiza, but only single hydranths; whereas hydranths only rarely form as lateral branches of the stalk, in place of a gonophore.

In an old hydranth as many as fifteen gonophores may be present, the youngest near the hydranth base being in early stages of devolpment, those in the middle zone being close to or actually functional, and those near the base of the stalk being represented mainly by stumps within a persisting perisarc.

Female Gonophores

Gonophores first appear at the base of the hydranth at the region where the hypertrophied gastrodermis of the hydranth thins down to that characteristic of the coenosarc. They arise one at a time as a two-layered protrusion of the body wall. The entocodon, which is apparently of epidermal origin, arises relatively early. By the time the next in series is starting to form, a given gonophore has its entocodon differentiated almost entirely into about eight or ten oocytes. The more opaque endodermal component becomes somewhat pointed at the center, foreshadowing the spadix (Fig. 2B). With further growth the spadix forms a high cone, reaching to the distal epidermis of the gonophore (Fig. 2C). At its maximum size (Fig. 2D), the oocytes are full grown with the germinal vesicle of each lying in the part farthest away from the spadix. The gonophore stalk is greatly lengthened and is about twice as long as the diameter of the gonophore proper. Rhythmical movements or a writhing of the gonophore commences at this stage, at least under the conditions of microscopic examination. The contained eggs change shape with the movements and may appear themselves to be responsible for them, but a close examination reveals the activity to reside in the layer of the gonophore wall immediately beneath the epidermis and derived from the entocodon. In mature gonophores the writhing movements and contractions of the wall culminate in its rupture distally (Fig. 2E). This rupture has two consequences. Distally, where the cells become greatly stretched and thinned out, rupture results mainly in their disaggregation, so that instead of withdrawing as a sheet they remain as isolated spherical cells scattered over the sticky surface of the ripe eggs. The proximal part of the wall however does withdraw towards the base of the spadix, leaving the latter naked and still holding on to the eggs by adhesion. At the same time the epidermis, with its tension now released, contracts down the stalk, and where the stalk narrows the epidermis becomes somewhat thickened and wrinkled (Fig. 2F, G). The eggs are fertilized and undergo their cleavage and development up to the planula stage ad-

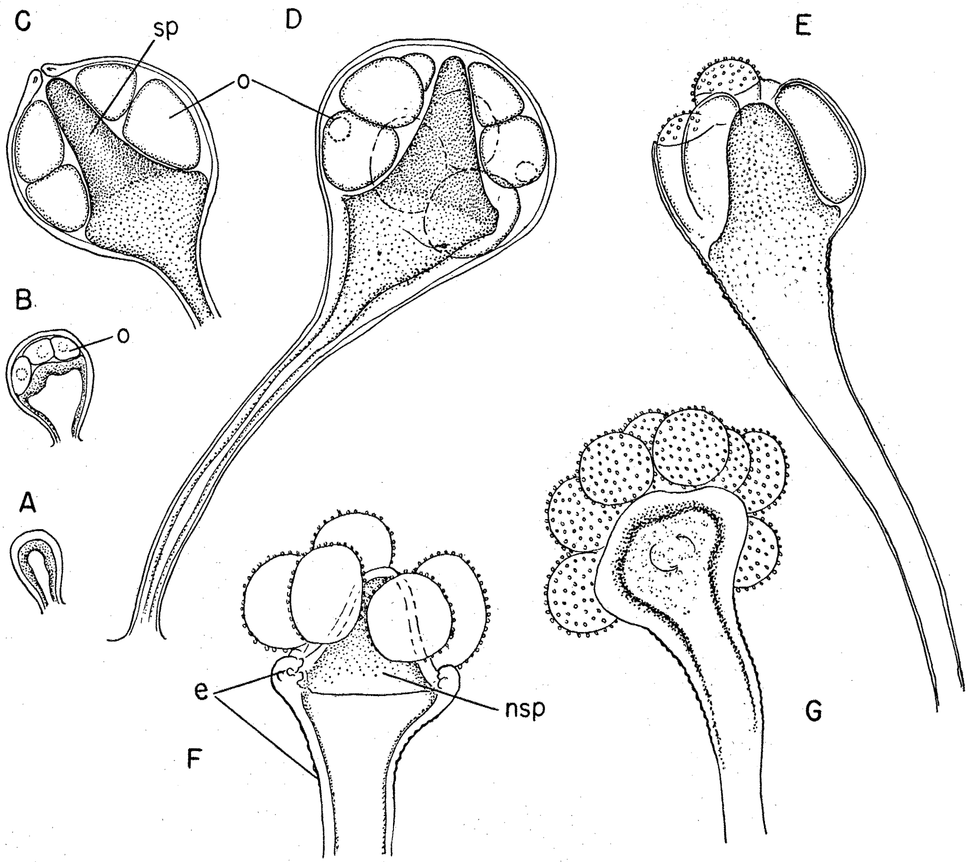

FIGURE 2. Female gonophores. A, young gonophore before appearance of entocodon. B, after segregation of ova from entocodon. C, D, fully formed gonophores with large ova and well developed spadix and long stalk. E, distal disintegration and rupture of epidermis, and basal epidermal contraction. F, G, matured gonophores with fully retracted epidermis, bearing fertilized eggs attached to the denuded spadix. e, contracted epidermis; nsp, naked spadix; o, ova; sp, spadix.

hering to the gonophore spadix, remaining there until able to move away as a result of their own efforts. Planulae on the point of departure are shown in Figure 1B, C and Figure 4A. Throughout their development on the spadix, an internal active hydroplasmic streaming is maintained within the lumen of the spadix. Whether of course this streaming is of any value to the developing eggs is difficult to determine.

Male Gonophores

The male gonophores develop as do the female, and have essentially the same appearance. Early stages showing the entocodon and the formation of the spadix are shown in Figure 3A and B. The lumen of the spadix alternately expands and

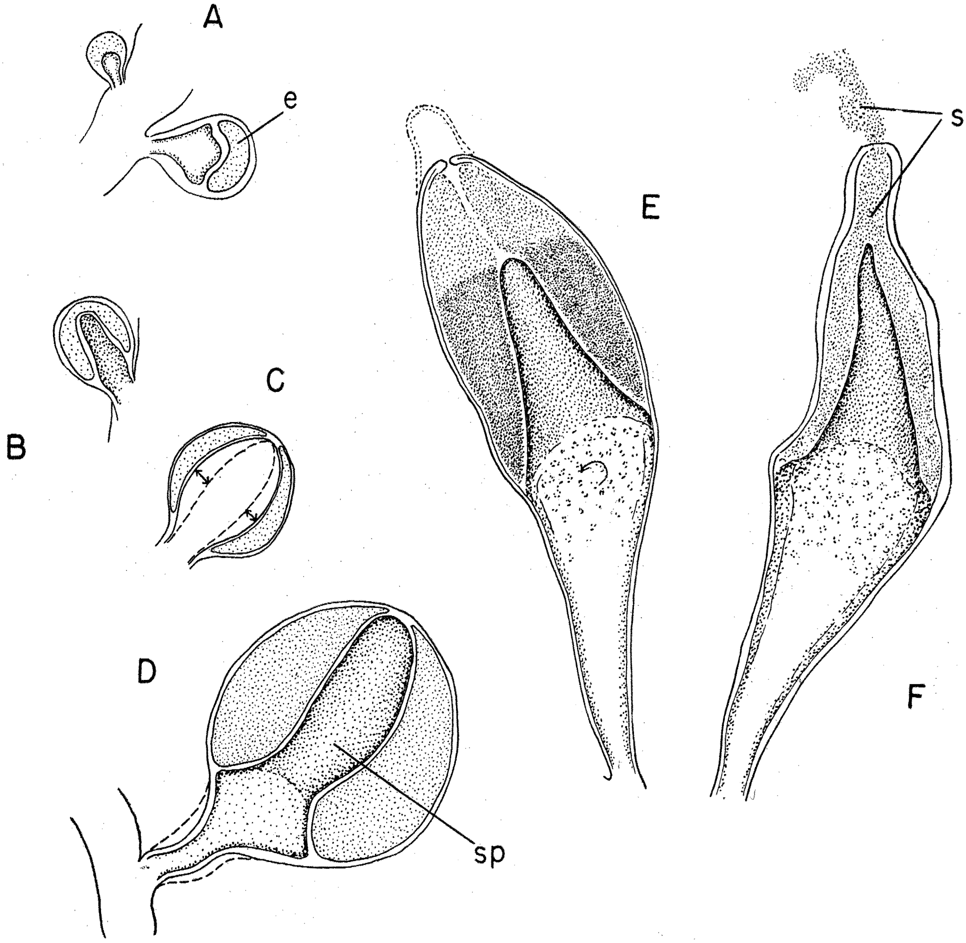

FIGURE 3. Male gonophores. A, B, young stage showing formation of entocodon and germ mass. C, later stage with arrows indicating expansion-contraction amplitude of spadix. D, late stage with germ cells present as spermatids, and broken lines indicating stalk diameter when dilated. E, ripe gonophore with active spermatozoa and expanding and contracting distal end. F, emission of spermatozoa. e, entocodon; sp, spadix.

contracts in a regular manner, with an amplitude indicated by the arrows in Figure 3C. In the later stages (Fig. 3D) the dilatation and contraction is more obvious in the short stalk of the gonophore, the growing mass of male germ cells possibly inhibiting or at least reducing the freedom of movement of the spadix wall itself.

With the attainment of full size, not only is the stalk relatively long, but the distal part of the gonophore also elongated. This is due on the one hand to the contractile property of the wall of the mature gonophore, and on the other to the pseudo-fluid quality of the mass of ripe germ cells. There is a rhythmical contraction of the gonophore wall similar to that of the female gonophore, but here resulting in an alternation between the stages indicated in Figure 3E. Finally the contractions culminate in rupture at the extreme distal pointed end, and the consequent escape of mature spermatozoa, shown escaping in Figure 3F.

Liberation of Eggs and Sperm

Both mature eggs and spermatozoa are liberated in essentially the same way, even though the eggs are not actually set free in the process. Rhythmical contractions of the gonophore wall result in its rupture distally. The contractions in each case are due to the activity of the tissue immediately subjacent to the epidermis, which must be regarded as homologous with the muscle layer of the free-swimming medusae of species of Bougainvillia.

Spawning in hydroids is usually associated with dawn (Lowe, 1926) or dusk, and not with darkness. Yet most of the ripe gonophores were examined at night and most of them ruptured within five minutes of first being exposed to the micro-

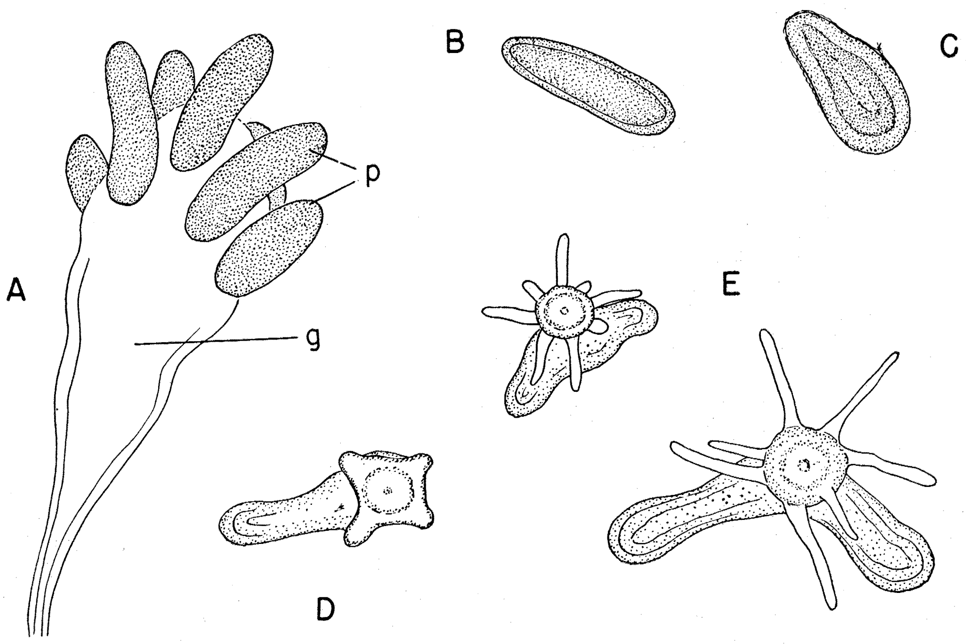

Figure 4. Development of planula. A, planulae about to swim away from gonophore. B, free-swimming planula. C, planula after about 24 hours, changing shape and losing ciliation. D, 12 hours after attachment, with stolon and 4-tentacled hydranth. E, two individuals 24 hours after attachment, with bipolar stolon on hydrorhiza and 8-tentacled hydranth. g, gonophore; p, planula.

scope light. It appears probable therefore that the stimulus of light evokes the contractions of the muscle layer, and spawning inevitably follows.

Settling of the Planula

Planulae escape from their adhesion to the spadix only as they become ciliated and active. A set about to launch forth is shown in Figure 4A. A planula swims for about 24 hours as a ciliate organism, and then becomes progressively pear-shaped (Fig. 4C), at the same time resorbing the external coat of cilia. About 12 hours after settling, a hydranth and stolon are already differentiated (Fig. 4D), four tentacles emerging in the first place. Twenty-four hours after settling, four intermediate tentacles are usually well formed, or a total of eight, while stolonic growth is bipolar, growing in opposite directions from the base of the hydranth along the substratum (Fig. 4E).

Summary

A new species of a hydroid genus not previously recorded from the Atlantic coast, *Aselomaris michaeli*, is described. The development and activity of both male and female gonophores are described in detail, together with settling of the planula and formation of the first hydranth.

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