

Giant nerve axons and escape swimming in *Amphogona apicata* with notes on other hydromedusae¹

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The trachyline medusa *Amphogona apicata* (family Rhopalonematidae) possesses giant axons and other special features previously described in *Aglantha digitale* and shows similar escape-swimming and slow-swimming responses. A review of the literature and new observations on several species suggest that, with the possible exception of members of the Ptychogastridae, these locomotory adaptations are peculiar to certain rhopalonematid hydromedusae.

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La méduse trachyline *Amphogona apicata* (famille Rhopalonematidae) possède des axones géants de même que d'autres caractéristiques particulières à *Aglantha digitale*; elle manifeste également les mêmes réactions de nage rapide et de nage lente. La révision de la littérature et de nouvelles observations sur plusieurs espèces permettent de croire que, à l'exception possible de certains Ptychogastridae, ces adaptations locomotrices sont particulières à certaines hydroméduses rhopalonématidées.

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Following the report by Singla (1978) of giant axons in the subumbrella of the trachyline medusa *Aglantha digitale*, this species has been intensively studied from the behavioural–physiological point of view (Donaldson et al. 1980; Kerfoot et al. 1985; Mackie 1980; Mackie and Meech 1985; Roberts and Mackie 1980; Singla 1983; Weber et al. 1982). The earlier observation that *Aglantha* can swim in two modes (Gladfelter 1973) has been confirmed. Fast, or escape, swimming is a response to tactile stimulation. It consists of one or a short series of powerful contractions involving the entire subumbrellar muscle sheet. One contraction can propel the animal through five body lengths. Slow swimming on the other hand is exhibited spontaneously as part of normal locomotion and feeding behaviour and consists of relatively weak, rhythmic pulsations in which only a portion of the muscle field is excited. One contraction propels the animal only about one body length.

In *Aglantha*, escape swimming is mediated by a system of rapidly conducting giant axons: a single-ring giant forms a closed loop around the lower margin of the bell and synapses upon eight motor giants, which run up the subumbrella, spreading excitation to the muscles via a system of lateral neurons. Slow swimming was originally thought to be spread by a separate system of finer nerves, but we now know that it too involves the motor giant axons (Mackie and Meech 1985). These remarkable axons are so far unique in the animal kingdom in being able to conduct two sorts of impulse. In slow swimming they conduct slow, calcium-dependent action potentials, while in the escape response they conduct fast sodium spikes.

The existence of these novel adaptations in *Aglantha* raises the question of whether or not comparable features exist in other medusae. We here present evidence that several members of the Rhopalonematidae, in particular *Amphogona apicata*, show the same structural and behavioural adaptations as *Aglantha*.

Observations on *Amphogona apicata*

Five specimens of this medusa were observed in their natural habitat at depths of 633–658 m during a series of dives in October 1984 with *Sea Link II* south of Chub Bay, Bahamas. Two specimens were collected from the submersible by methods described in Youngbluth (1984) and were brought to the surface for study and photography (Fig. 1A) in tanks on board a companion vessel, R.V. *Cape Florida*.

The two captured specimens had bells ca. 5.5 mm tall. Both were sexually mature males and colourless. At rest they hung motionless with tentacles extended. They appeared to be neutrally buoyant. Both medusae exhibited bouts of slow swimming in which the tentacles either trailed behind or were held partially contracted in a spiral configuration, as in *Aglantha*. In the fully relaxed state, the tentacles were held out around the sides, defining a roughly hemispherical space underneath.

Escape swimming was evoked by touching the bell margin.

The response consisted of one to three powerful contractions, each of which propelled the animal several body lengths.

A specimen preserved in 5% formalin in seawater was sectioned for electron microscopy. Though swollen and vacuolated in parts, the tissue was fixed well enough for the giant axons and other important features to be readily identified (Fig. 1B).

Like *Aglantha*, *Amphogona* has eight motor giant axons running radially from the margin up to the apex of the subumbrellar cavity. Lateral neurons run out over the striated muscle sheet which they innervate at scattered neuromuscular synapses. Accompanying each motor giant axon is a bundle of conventional, small-diameter radial neurites (Fig. 1B). A ring giant axon is present near the outer nerve ring but in our material it shows signs of osmotic damage and appears to have collapsed and to have lost most of its contents. A large axon runs down the dorsal side of each tentacle as in *Aglantha*. The size relationships of these components are commensurate with measurements made on small specimens of *Aglantha*.

Thus, *Amphogona* resembles *Aglantha* in showing two sorts of swimming and in possessing the same unusual nerve circuitry.

Occurrence of similar adaptations in other medusae

A considerable body of information, reviewed by Spencer and Schwab (1982), exists on the neuromuscular organization and behaviour of representatives of the Anthomedusae, Leptomedusae, and Limnomedusae. In none of these, nor in the olindiad species *Gonionemus vertens* and *Eperetmus typus* (Carolsfeld 1984), is there any indication of the special neural structures in question or of two sorts of swimming. Narnomedusae have not been investigated electrophysiologically, but histological studies on *Cunina* spp. and on *Solmundella bitentaculata* (as *Aeginopsis mediterranea*) by Hertwig and Hertwig (1878) show no giant axons. We have observed only one swimming mode in specimens of *Solmissus marshalli* and *Aegina citrea* at Friday Harbor and in the Bahamas.

Kramp (1961) recognizes five families in the suborder Trachymedusae of which the Rhopalonematidae, to which *Aglantha* and *Amphogona* belong, is the largest. *Rhopalonema velatum* itself was studied by Hertwig and Hertwig (1878). These authors show a structure near the outer nerve ring which they refer to as a "fluid filled space," a fair description of the appearance of the ring giant axon in cross section. In the position where we would expect to find the motor giants, they describe "radial fibre tracts," which they could not identify with certainty, but which they suggest are muscle bands similar to those seen in geryonids. It is at least as likely that the tracts in question are actually a composite of the motor giant axons and the closely associated fine radial nerve fibres, as seen in *Aglantha* and *Amphogona*. All three of these species and *Aglaurea hemistoma* (also studied by Hertwig and Hertwig, 1878) show every sign of close relationship right down to fine structural details. For instance, they all have paired "comb pads"

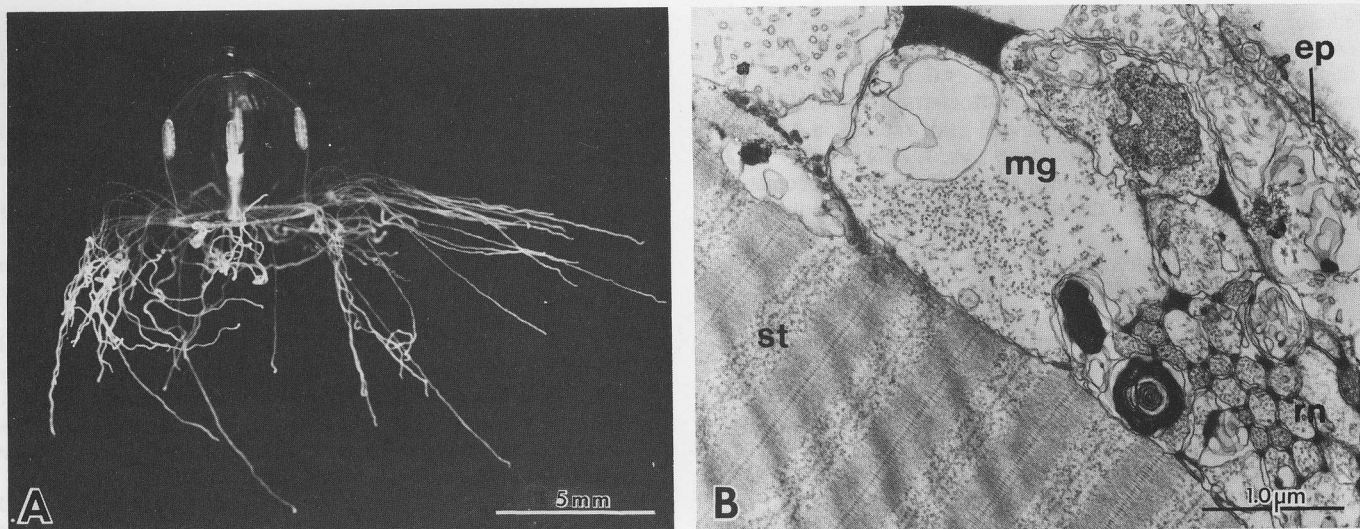


FIG. 1. (A) *Amphogona apicata*. Living specimen measuring 4.5 mm in bell diameter and 5.5 mm in bell height. Photographed in a shipboard aquarium within a few hours of collection. (B) Section through subumbrellar ectoderm at right angles to radial axis. *ep*, epithelial surface; *mg*, motor giant axon; *rn*, bundle of small radial neurites; *st*, striated myofibre.

(Singla 1983) close to the outer marginal nerve ring, which are distinctive sensory structures found only in this group of medusae. Hertwig and Hertwig (1878) do not mention a fluid-filled space or radial fibre tracts in *Aglaura*, but they give relatively little attention to this species. The ring giant axon might have been hard to see in their material, as it tends to collapse, as we found in *Amphogona*. The likelihood that *Aglaura* possesses escape circuitry is strengthened by our observation of living *Aglaura hemistoma* at Leigh, New Zealand, in October 1981. These medusae also showed two sorts of swimming, much like *Aglantha*.

The only other rhopalonematid that has been studied sufficiently to deserve mention is *Pantachogon*. A minute species of *Pantachogon*, possibly *P. scotti*, has been observed from the submersible *Pisces IV* in many locations in the Strait of Georgia, British Columbia, and adjacent fjords, generally below 125 m. These medusae were observed to perform bursts of extremely rapid, powerful swimming. Gladfelter (1973) describes swimming in *Pantachogon haeckeli* as the most powerful seen in any medusa. Nevertheless, nothing equivalent to slow swimming has been described and giant axons have not been found in electron microscope sections of the small local species.

Lastly, considering the four remaining families of trachylinae medusae, we have found no clear evidence for an escape-swimming system in any case. Not enough is known about the Petasidae for any judgement to be made. We have observed four species of Halicreatidae (*Halicreas* sp., *Halicera conica*, *Halicera* sp., and *Halitrepes maasi*) from *Sea Link II* and in a shipboard aquarium. None showed two modes of swimming. The Geryonidae are well known from studies by Hertwig and Hertwig (1878) and several later authors (reviewed in Bullock and Horridge 1965; Spencer and Schwab 1982). They have no escape-swimming response and only one mode of swimming (bursts of rapid, powerful pulsations, not unlike *Pantachogon*). Hertwig and Hertwig (1878) show fluid-filled spaces in the margin of *Geryonia proboscidalis* (as *Carmarina hastata*), but these lie in the inner nerve ring and are almost certainly the large swimming motor neurons found in this location in most hydromedusae (Satterlie and Spencer 1983). We have exam-

ined formalin-fixed *Liriope tetraphylla* (Geryonidae) from the equatorial Atlantic by electron microscopy and can confirm that ring and motor giants are absent. *Tesserogastrina muscicola* and *Ptychogastrina polaris* (family Ptychogastridae) are epibenthic species, spending much time on the bottom. They seem to swim only when stimulated or disturbed (Hesthagen 1971). We have cut sections of *Tesserogastrina* from Oslo fjord (kindly sent by Dr. I. H. Hesthagen) but could find no giant axons by electron microscopy. However, better preserved material would be needed for certainty on this point. The Ptychogastridae are an interesting group because, when they do swim, they swim strongly and the response seems to be a form of escape behaviour. Thus, it is possible that their swimming corresponds to escape swimming in *Aglantha* and that their capacity for "normal" swimming has been lost or reduced. Of all the trachylinae, they show the closest structural similarities to the rhopalonematids. It would therefore be desirable to study these medusae more thoroughly.

At the present time, we can conclude that at least one other rhopalonematid medusa (*Amphogona apicata*) has the same escape-swimming system found in *Aglantha*, that *Rhopalomena* and *Aglaura* probably also have these adaptations, and that in medusae other than the Rhopalonematidae, with the possible exception of the Ptychogastridae, no such adaptations have evolved.

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