

Evolution of the Chondrophora: Evidence from Behavioural Studies on *Vevelia*

W. GORDON FIELDS AND G. O. MACKIE

Department of Biology
University of Victoria, Victoria, B.C.

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The chondrophore *Vevelia* shows concert behaviour closely resembling and presumably homologous to that described for *Porpita*, *Pelagozydra*, and for the sessile tubularian hydroids *Tubularia* and *Corymorphida*. The movements consist of orally directed tentacular flexions, accompanied by retraction of the blastostyles, along with muscular contractions in the mantle and in the crest surmounting the sail. Concerts may consist of single contractions or sequences of contractions, the latter sometimes summing to produce a sustained declination of the tentacles or contraction in the other parts. Concerts are repeated periodically at intervals of between 1 and 3 min.

Electrical potentials (concert pulses) are recorded from all parts of the body surface at each concert contraction. The potentials are through-conducted at 30-35 cm/sec in parts of the aboral surface. Feeding changes the concert pattern, introducing a type of event called a feeding pulse. Peristalsis in the proboscis, as in *Tubularia*, is exhibited without electrical concomitants.

The observations support the view of *Vevelia* as a large individual hydroid in no way comparable to a siphonophore. It is regarded as a floating tubularian hydranth with inverted stem. *Vevelia* and *Porpita* (family *Velellidae*) are assigned to the superfamily *Tubularoidea*. The freshwater hydra shows a type of behaviour resembling modified tubularian concerts, and its possible affinity with the tubularoid group is discussed.

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Les chondrophores du genre *Vevelia* exhibent un comportement de synchronisme semblable et probablement homologue à celui déjà décrit chez *Porpita*, *Pelagozydra* et chez les hydroïdes tubulaires sessiles *Tubularia* et *Corymorphida*. Les mouvements consistent en des flexions des tentacules vers la bouche, accompagnées d'une rétraction des blastostyles et de contractions musculaires du manteau et de la crête surmontant la voile. Les mouvements synchrones peuvent être de simples contractions ou des séquences de contractions dont la sommation produit parfois soit un abaissement soutenu des tentacules, soit une contraction, également soutenue, des autres parties du corps. Les mouvements synchrones se répètent périodiquement à intervalles de 1 à 3 min.

Des potentiels électriques (influx synchrones), détectés dans toutes les parties du corps, accompagnent chaque contraction synchrone. Les potentiels sont transmis par réseau continu aux parties de la face aborale à une vitesse de 30-35 cm/sec. L'absorption de nourriture modifie les caractéristiques de l'influx synchrone et donne naissance à ce qu'on appelle l'influx alimentaire. Comme chez *Tubularia*, les mouvements péristaltiques du proboscis se produisent sans phénomènes électriques concomitants.

Ces observations sont en accord avec le point de vue que *Vevelia* est un grand hydroïde individual, d'aucune façon comparable à un siphonophore. Nous le considérons comme un hydranth flottant de tubulaire à tige renversée. Nous assignons *Vevelia* et *Porpita* (famille des *Velellidae*) à la super-famille des *Tubularoidea*. L'hydre d'eau douce a un comportement semblable aux mouvements synchrones des tubulaires. Nous analysons son affiliation possible au groupe des *Tubularoidea*.

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THE systematic status of *Porpita* and *Veabella* has long been debated. These organisms have been regarded as modified medusae, as hydroid colonies related to siphonophores, and as hydroid individuals. Most textbooks still treat them as a subdivision of the order Siphonophora, although modern specialist opinion has moved completely away from this position. *Porpita* and *Veabella* are excluded from the order Siphonophora in the two major accounts of that group published in recent years (Totton 1965; Stepan'iants 1967). Most specialists favour a relationship with sessile hydroids rather than with siphonophores. Totton (1954) and Rees (1957) recognized an affinity with athecate hydroids, but assigned *Porpita* and *Veabella* to a separate order, Chondrophora. Picard (1955) classified them as a family (Vellellidae) within the athecate hydroids having an affinity with *Zanclea* and *Pteroclava* (family Zancleidae, Rees 1957). Brinckmann (1964) also favoured a position in the Athecata but as a superfamily of capitate hydroids with tubularian affinities. In this view she followed Agassiz (1883), Leloup (1929), Garstang (1946), and Mackie (1959, 1960), who on various grounds stressed the tubularian homologies of the chondrophores.

If *Veabella* is to be regarded as a hydroid, is it a hydroid individual or is it a colony? Conventionally, it is regarded as a colony, with gastrozooid, gonozooids, and dactylozooids representing individual polypoid types within the colony. Alternatively, it can be regarded as a single large tubularian

hydranth. Figure 1 illustrates the latter view. The large central structure bearing the main mouth at its tip is homologized with the proboscis of a sessile hydroid like *Tubularia* or *Corymorphida*, and is thus considered to be part of the primary hydranth rather than being a separate individual, or "gastrozooid." It will here be called the proboscis. The outer fringe of tentacles corresponds to the main (proximal) circle of tentacles in the sessile tubularian, rather than representing dactylozooids. There is no homologue to the small distal tentacles of *Tubularia*. The medusae belong to the Haeckelian family Codonidae, which are characteristic of capitate hydroids, including those tubularians having free medusae.

The structures on which the medusae are borne prior to their release are, in *Porpita* and *Veabella*, long mobile appendages with an opening at the tip through which food can be ingested. Adherents to the colonial view argue that these structures are a separate class of polyp individuals, the gonozooids. However, they occupy a position corresponding to that of the blastostyles or racemes of the sessile tubularian, and can be regarded as blastostyles having a secondarily developed oral aperture. This view was adopted by Mackie (1959) and by D. V. Naumov (1961, cited in Stepan'iants 1967), who accordingly regard the reproductive appendages not as individuals in a colony but as out-growths from the hydranth wall of single hydroid individuals.

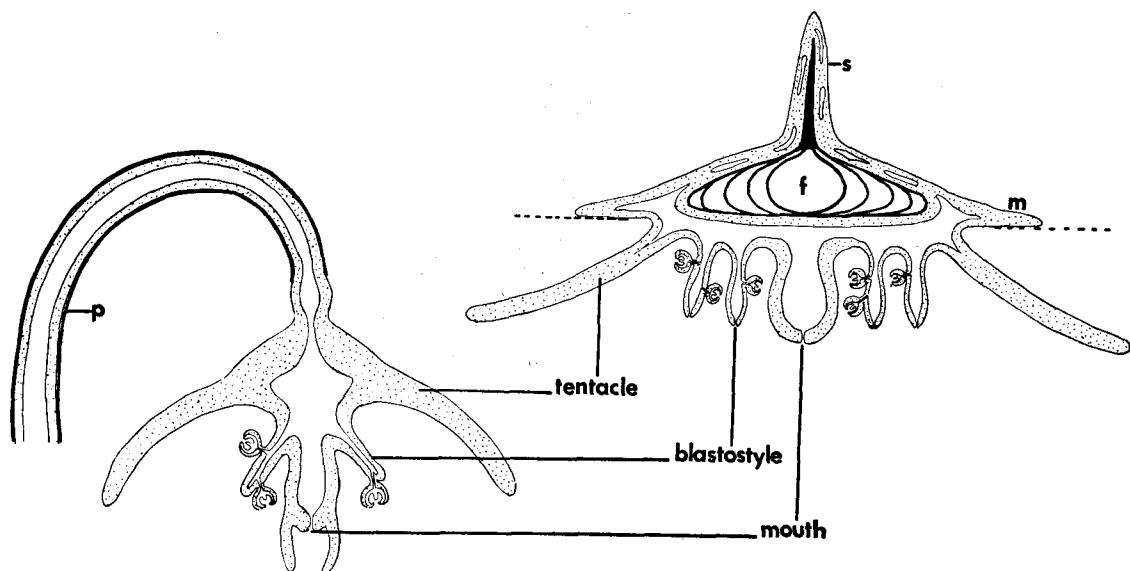


FIG. 1. A chondrophore (right) compared with a sessile tubularian hydroid (left). For explanation, see text.

Although we accept this view, we should point out that the *Velella* hydranth is a highly specialized one. It floats upside down at the surface instead of sitting on a stalk attached to the bottom. During development, the aboral pole of the larva grows inward forming the first float chamber (Fig. 1, f) instead of growing out to form the stem. The invaginated ectoderm layer then secretes a series of secondary float chambers concentric with the first. These layers of chitin presumably correspond to the layers that form the perisarc (Fig. 1, p) of the sessile hydroid, but the whole structure is inverted.

Surrounding the hydranth just above the tentacles, an outfolding develops at an early stage. This structure, the mantle, (Fig. 1, m) has no homologue in the sessile tubularian. It has a water-repellent upper surface and normally lies flat on the surface film, where it appears to act as a stabilizer.

The aboral sail (Fig. 1, s) again has no counterpart in the sessile hydroid. It is set asymmetrically across the top of the float, so that the animal is blown at an angle to the wind and not directly downwind (Mackie 1961; Savilov 1961). In its ability to sail at an angle to the wind and in the existence of mirror-image dimorphism, *Velella* resembles the siphonophore *Physalia*, but these resemblances appear to be entirely convergent, representing independent adaptations to conditions in the rather unusual environment at the air-water interface that they share (Mackie 1961).

Considerable attention has been given to hydroid behaviour in the last decade, with the development of new and specialized electrophysiological recording techniques. We now have detailed records of the electrical concomitants of behaviour in *Hydra* (Passano and McCullough 1964, 1965; Josephson 1967; Rushforth 1967, 1971), *Cordylophora* (Josephson 1961; Mackie 1968), and *Tubularia* (Josephson 1962, 1965; Josephson and Mackie 1965; Josephson and Uhrich 1969). If the chondrophore is indeed a modified individual hydroid, its behaviour should be expected to show resemblances to that of the sessile hydroids to which it is most closely related, and similar electrical patterns should be obtainable in the two instances. A previous study on *Porpita* (Mackie 1959), made before electrical recording techniques had been brought to bear on hydrozoan behaviour, showed apparent behavioural homologies with sessile forms such as *Corymorpha* and gave support to the view that *Porpita* is an individual rather than a colony. We have now observed the behaviour of *Velella* and recorded correlated electrical activity. This new work strengthens the homologies previously proposed.

Materials and Methods

Velella velella L. is abundant in the North Pacific (Savilov 1961) and specimens are frequently washed ashore along the coast from California to northern British Columbia. They occasionally penetrate Juan de Fuca Strait, a major invasion taking place in 1946 when considerable numbers reached Victoria (Carl 1948).

Specimens collected near Sooke, B.C., on April 12, 1970, were placed in glass-covered tanks maintained at 15 C. Since the sails wither in dry air, the humidity of the air beneath the glass was raised by bubbling air through the water in which the animals were floating.

To record electrical events, equipment similar to that used in previous studies on hydroid behaviour was employed (Josephson 1965). In addition to recordings made in the open tanks, recordings were made from specimens in small dishes in a Faraday cage.

On May 7, 1970, some specimens were collected at Asilomar Beach, Pacific Grove, California, and studied at the Hopkins Marine Station, where they were kept in the tanks at 12.4 C. Their activities were recorded on 16-mm movie film. In some sequences, a mirror was arranged to give a simultaneous view of the animals from the side and from below. The films were used in the analysis of behaviour, particularly in the measurement of contraction frequencies. Figure 2 is taken from these movie sequences. Finally, specimens were collected from the open ocean during a cruise on the C.N.A.V. *Laymore* off the Oregon coast, and their behaviour was observed in the laboratory on June 27, 1970.

Results

"CONCERT" BEHAVIOUR

The term "concerts" (Josephson and Mackie 1965) refers to rhythmically occurring events in *Tubularia*, in which the tentacles flex orally in one or a series of synchronized contractions. The term is here applied to similar events in *Velella* and other forms.

In *Velella* concerts, the tentacles flexed orally and, at the same time, the blastostyles shortened symmetrically, and the mantle contracted in the downward (oral) direction. Vogt (1854) observed these movements but did not relate the mantle movements to synchronous events in the tentacles and blastostyles. In some specimens from the *Laymore* cruise, the soft tissues forming the crest on top of the sail contracted in synchrony with the other active parts. At the two ends of the crest, movement was away from the longitudinal axis of the float; thus, the effect of crest contraction was to increase the asymmetry of the sail with respect to the float. Some variation was observed in the intensity with which concert components were expressed in different individuals. Mantle depression was seen only when a portion of the

mantle had fallen below the water surface and was thus free to move (Fig. 2). Normally, with the mantle held flat on the surface, mantle contractions accompanying concerts resulted in no detectable degree of depression.

Concerts consisted of single contractions or sequences of contractions. The contracted parts started to relax immediately following a contraction. In the case of the tentacles, the distance moved in the aboral direction between contractions closely approximated to the distance moved in the oral direction during contractions. In the early stages of a concert sequence, contractions tended to sum and to produce a marked degree of depression of the tentacles. However, an equilibrium point was then reached, with the oral and aboral movements balancing each other. At the close of the sequence, the tentacles and other parts returned to their relaxed positions. The contraction frequency required to maintain the tentacles in a strongly depressed position with the tips curled around under the float as in Fig. 2 was about 1/sec as measured from movie sequences. Frequencies as high as 1.3/sec were observed in one specimen at the height of a concert. In such instances, the to and fro movements of the tentacles were barely discernible, the contractions having assumed a tetanuslike character. Such sustained contractions lasted up to 15 sec. Pulse frequencies in typical concerts showed a pattern of acceleration from a slow start, with some deceleration at the end. These changes in tempo were much less dramatic than those described in *Porpita* (Mackie 1959).

In the specimens examined, not all tentacles took part in concerts. Of those that did, some contracted more strongly than others. As in *Porpita*, a few tended to join in late, after the others had achieved some degree of declination. However, whether they started late or early, or contracted strongly or weakly, all active tentacles showed synchrony during concerts.

Like the tentacles, the blastostyles often reached a tetanic condition, with the component contractions not separately distinguishable to the naked eye. The same was true to a lesser degree for the mantle.

Peristaltic movements were observed in the proboscis, but they showed no temporal relation with concerts. In one specimen showing concerts every 170–190 sec, peristalsis occurred every 34–45 sec.

Concert periodicity in *Velella* varied roughly from 1 to 3 min, but tended to remain fairly constant for any given individual over periods of an hour or more. Concert behaviour was neither induced nor inhibited by photic stimulation. In this respect

Velella resembles *Tubularia*, but differs from *Pelagothrya* (Pilgrim 1967a, b), which is extremely light-sensitive, responding to a sudden reduction in illumination by vigorous concert activity.

ELECTRICAL CORRELATES OF BEHAVIOUR

As in *Tubularia*, concerts in *Velella* are accompanied by electrical signals in the millivolt range. They are frequently composite events. The predominant polarity is negative (up) in recordings from the aboral side.

Single oral flexions of the tentacles were accompanied by single pulses, sequential contractions by a series of such pulses (Fig. 3, 4). Not all pulses were accompanied by a visible contraction, especially during concerts of long duration, when the contractions had summed to produce a noticeable degree of declination.

Concert pulses were recorded in some tentacles that were not visibly taking part in the concert, as well as in active ones, but they were recorded at higher amplitudes in the latter (Fig. 5). The pulses were also recorded in the blastostyles, in the proboscis, in the mantle, and all over the aboral surface including the sail and its crest (Fig. 6), and appear to be propagated throughout the whole animal. They appear in different places in slightly different time relations, showing that they are being actively propagated. It is not clear where the pulses originate. Variations in the shape of the pulses recorded at the same point suggest that impulses may be arriving from more than one direction and presumably are therefore being generated at more than one site. Multiple, interacting pacemakers seem to be a fundamental part of the behavioural organization in hydrozoans (Passano 1963).

Electrical stimulation of any of the regions in which concert pulses can be recorded resulted in the generation of propagated pulses similar to spontaneous concert pulses (Fig. 7). Conduction velocities measured in the circular direction on the aboral surface are in the order of 30–35 cm/sec at 15°C.

One specimen of *Velella* was fed on pieces of fish muscle during a long-term recording of its concert activity. The typical electrical activity of this specimen prior to feeding consisted of regular single concert pulses at 75 sec periodicity. For over 15 min following feeding, a new pattern of signals was in evidence (Fig. 8), replacing the former pattern completely for about 11 min, following which the original pattern began to reemerge. Active peristalsis was observed in the proboscis later on, but no electrical events could be associated with this activity, even when electrodes were attached directly

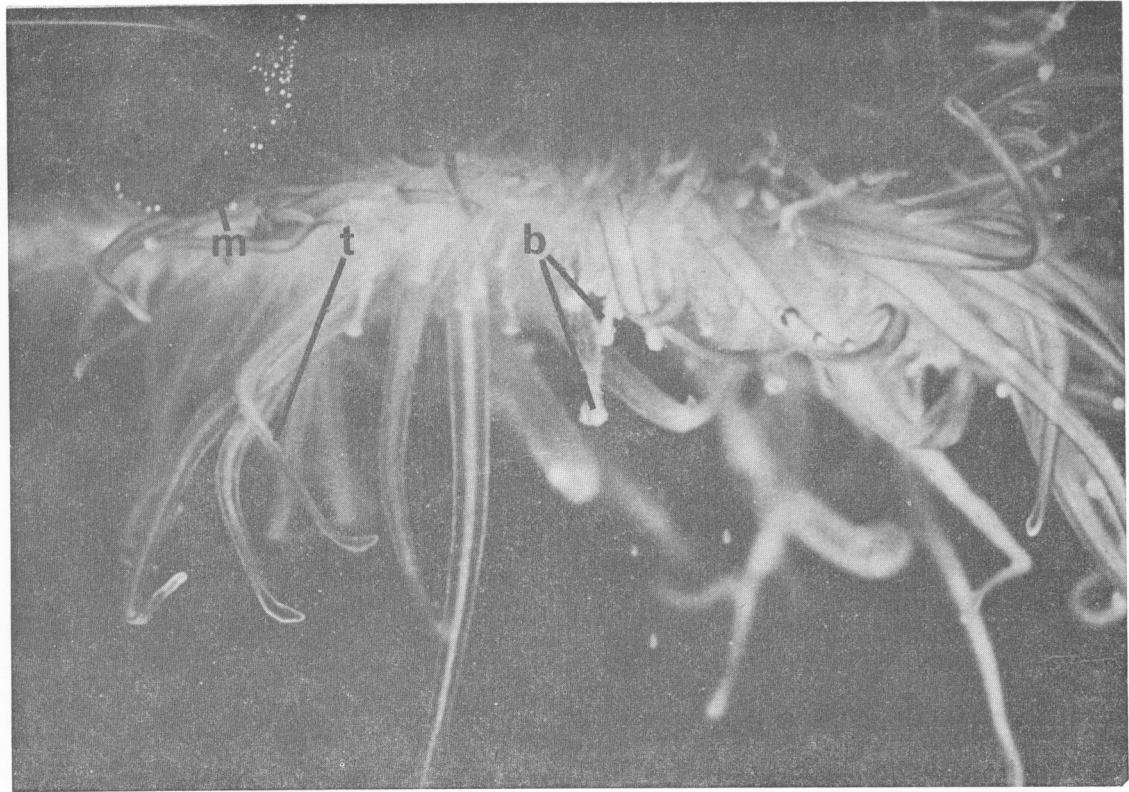


FIG. 2. A *Velella* in the middle of a concert, seen from the side below the waterline. The tentacle tips (*t*) are bent round in the oral direction, most of the blastostyles (*b*) are retracted, and a portion of the mantle (*m*), which has dipped below the surface, has bent in the oral direction.

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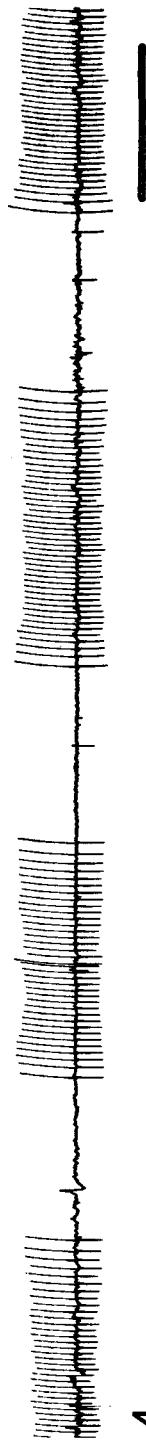
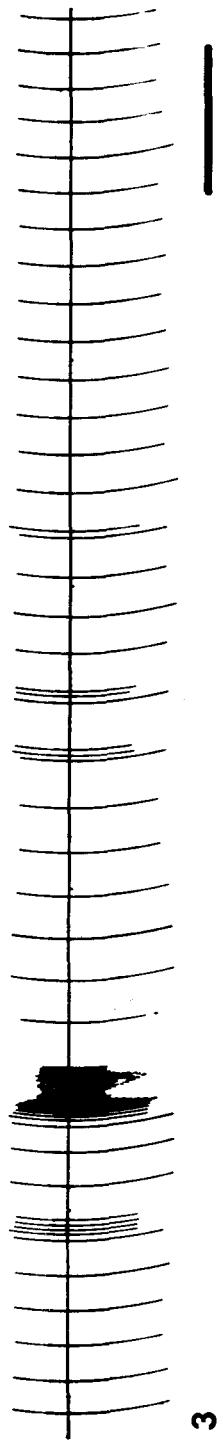


FIG. 3, 4. Records of concert activity in *Velella* made with a suction electrode attached to the aboral surface while the specimen floated in a container of cooled sea water. (Scales: 5 and 1 min respectively.) The specimen in Fig. 3 showed concerts consisting of single concert pulses roughly every 75-90 sec, with irregular periods of more intensive activity. The specimen in Fig. 4 showed concerts consisting of bursts lasting about 1½ min, each burst consisting of 35-45 pulses.

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to the proboscis. It is not clear if the "feeding pulses" represent events in the system responsible for spreading concert pulses, but stemming from



FIG. 5. Record of concert pulses from a tentacle, to show increased amplitude of pulses that occurs when the tentacle begins to flex (arrowhead) (scale: 3 sec).



FIG. 6. Three-channel recording from blastostyle (top), proboscis (middle), and mantle (bottom) to show synchrony of composite concert pulses in the three places (scale: 5 sec).

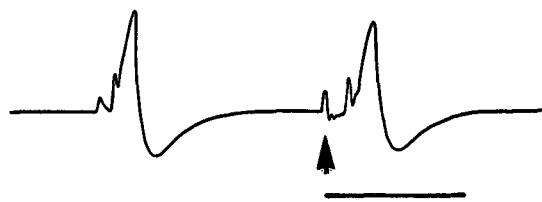


FIG. 7. Following a spontaneous concert pulse, a shock was delivered (arrowhead). The induced event resembles the spontaneous one. The recording and stimulating electrodes were both on the aboral surface (scale: 500 msec).

another pacemaker site, or originate in an entirely different conducting system. Mackie (1960) found histological evidence of two superimposed nerve plexuses in *Veabella*, but the significance of this double innervation remains unclear.

Discussion

The earliest allusion to a tubularian concert that we know of is that of Guilding (1828) for *Porpita* ("... praedam brachii quibusdam vel omnibus subito declinatis amplectens"). *Porpita* (Mackie 1959), *Tubularia* (Josephson 1962), *Corymorphida* (Parker 1917), and *Pelagothysdra* (Pilgrim 1967a, b) show basically similar activities, in which the tentacles are flexed from their normal position by one or a series of contractions to a position where they are more or less gathered in around the mouth. Synchrony of all active components is a general feature, and this has now been demonstrated in *Corymorphida* by E. Ball (unpublished data), a form earlier reported by Wyman (1965) to be exceptional in this regard. Concert periodicities vary in different forms. For example, *Porpita* concerts show a 30-sec periodicity, those of *Tubularia* falling within the range 10 sec to several minutes. In *Tubularia*, the pattern is influenced by nutritional state (Josephson and Mackie 1965). An example of a concert pattern from a recently fed *Tubularia* is shown in Fig. 9 for comparison with the *Veabella* records. We lack exact information regarding the influence of nutritional state on the concert pattern in *Veabella*, although some short-term effects of feeding have been demonstrated.

Despite variations in concert frequency and pattern, the overall resemblance of concerts in *Veabella* and *Porpita* to those in the sessile hydrozoans is evident. The concert can be regarded as a homologous behaviour pattern within this group of animals. This concept of behavioural homologies between chondrophores and sessile tubularians is fully consistent with the morphological and developmental evidence indicative of close systematic

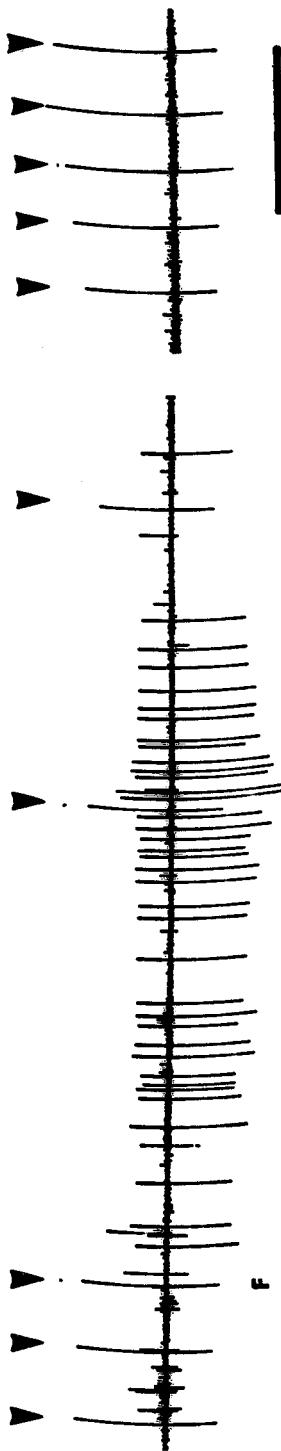
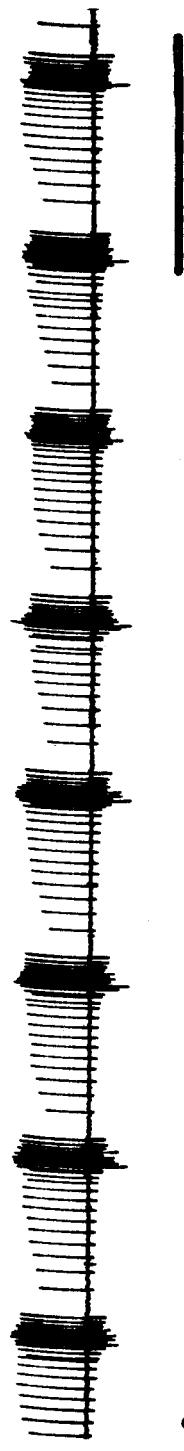
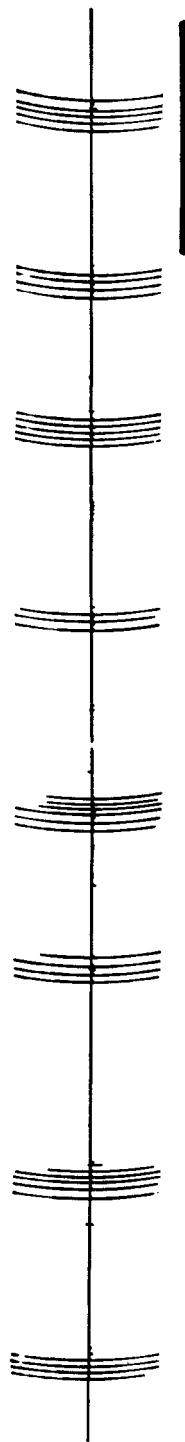


FIG. 8. Following the addition of food at point F, the pattern of concert pulses (arrowheads) is interrupted by feeding pulses. The gap in the record represents 8 min, after which the normal concert pattern was again shown (scale: 3 min).



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FIG. 9. Concert sequence in *Tubularia* recorded from the neck following feeding (scale: 1 min).



10

FIG. 10. "Concert" sequence in a fed hydra (contraction burst pattern) (scale: 5 min).

affinity between the two. If a chondrophore is an expanded tubularian hydranth, it would be expected to behave like one. We propose including the chondrophores within Rees' (1957) superfamily Tubularoidea. The classification becomes:

Order ANTHOMEDUSAE

Suborder CAPITATA

Superfamily TUBULAROIDEA

Family Corymorphidae (*Euphysa*, *Corymorpha*, *Branchiocerianthus*, etc.)

Family Tubulariidae (*Tubularia*)

Family Margelopsidae (*Margelopsis*, *Pelago-hydra*)

Family Velellidae (*Porpita*, *Velella*).

The true siphonophores (order Siphonophora) represent, in our view, a distinct line of evolution characterized by proliferation of polymorphically specialized, secondary polyps and medusoids from the oozooid, or primary zooid. These complex pelagic bud colonies cannot be accommodated within the Tubularoidea, although their nearest relatives may well lie in that group. Individual gastrozooids and palpons in *Nanomia cara* (a physonectid siphonophore) show behaviour reminiscent of concerts.

The nearest thing to a tubularian concert in any hydroid outside the Tubularoidea is in *Hydra* itself. Dr G. A. Shibley of Lawrence University, Appleton, Wisconsin, has photographed hydras in all stages of their periodic changes in shape. He finds (personal communication) a contraction sequence, involving first the longitudinal muscle of the ectoderm and then the circular muscle of the endoderm of the peduncle, a sequence recalling concerts in *Tubularia* where "neck" contraction corresponds to the second phase in hydra sequence. In both instances the contractions result in displacement of gut fluids toward the anterior end and are followed by downward peristalsis, which redistributes the fluids. Although concerted flexions of the tentacles do not occur in hydra, the contraction sequence otherwise resembles a tubularian concert and has similar electrical correlates. Is hydra descended from tubularian stock? Such a derivation seems preferable to the limnohydrine origins proposed by Bouillon (1968) and Dales (1970). Hydra's possession of stenoteles would seem to link it with capitate hydroids, siphonophores, and chondrophores rather than with the order Limnohydrina, where stenoteles are lacking.

Figure 10 shows a "concert" sequence performed by *Hydra canadensis*, a species that shows concert patterns consisting of one or few pulses,

the pattern being influenced by several environmental variables, including feeding stimuli (Rushforth 1971). These pulses accompany the initial contraction phase of the concert. As in *Tubularia* and *Velella*, peristalsis is not accompanied by recordable signals.

The functional significance of concerts is unclear. Several functions may be involved, as several action systems take part. In *Porpita*, the tentacular flexions were reported by Lesson (1843) to function in food collection. In *Velella*, however, the movements are not of sufficient amplitude to be interpretable in this way. In *Corymorpha*, Parker (1917) interpreted concerts as part of a food-collecting cycle, but E. Ball's observations (unpublished data) raise doubts in this regard. In *Tubularia* no food-collecting role has been postulated for the concert flexions.

Some workers have supposed the tentacular flexions to be locomotory, but Mackie (1959) denies any such function in *Porpita*, and Pilgrim's studies (1967a, b) give no support to Dendy's claim (1902) that *Pelago-hydra* rows itself through the water by the tentacular flexions. In *Velella*, the movements have no locomotory effect.

In *Tubularia* and *Hydra*, concert movements and accompanying peristalsis combine to bring about trituration of food in the gut and its dispersion. Concerts may have similar effects in *Velella* and *Porpita*, the trituration and dispersion being caused by contraction of the body wall musculature on the oral side, as evinced chiefly in the shortening of the blastostyles, rather than from the tentacular flexions, or contractions in the mantle and sail. These latter movements, like the tentacular flexions in *Tubularia*, would appear to be secondary manifestations, not functional in themselves.

Chun (1897) suggested that the concert movements in *Velella* constituted breathing movements. He envisaged the contractions as compressing the chitinous tracheae that run down from the float chambers into the tissues of the lower side, and as causing air movements within the whole system. The float chambers open to the atmosphere by aboral stigmatal pores. Schneider (1898) criticized this theory, but the matter has not been settled and merits further study. An air-breathing process might be especially useful in *Velella*, where the tissues harbor very large numbers of zooxanthellae.

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