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Swimming Gastropods (Opisthobranchia and Prosobranchia)

BY

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(20 Text figures)

INTRODUCTION

In looking for information about swimming gastropods, it became evident that clarification of the classification of the methods of swimming was necessary. Most authors have treated swimming behavior superficially, without a close look at the various types of swimming in the class Gastropoda. However, more attention has been given to individual species of late. For example, any number of gastropods has been described as undulating; yet there are at least 6 different ways of swimming. In this paper 3 of the undulators have been placed in a different category.

This is not the first attempt to categorize swimming in gastropods. Pelseneer (1935) outlined the swimming types for members of the phylum Mollusca, including Pelecypoda, pelagic species, and veligers. Pruvot-Fol (1954) also discusses locomotion in gastropods (pelagic species). These works have been useful in establishing swimming types for this paper.

A system of classification for 9 different forms of swimming is presented; the terms are defined. The knowledge regarding the swimming in *Coryphella cynara* and *Nembrotha eliora* is expanded. Introduced to the literature is a new swimmer, *Olivella zanoeta*. In Table 2 are listed 47 species of swimming opisthobranchs and 8 species of swimming prosobranchs.

It is not fully known why most of the swimming gastropods do swim. There is speculation that in many cases it is an escape response although the predator as yet is unknown. However, swimming is an escape response for *Nembrotha eliora* (from the predatory nudibranch *Roboastra* sp.) and for *Olivella biplicata* (from the echinoderm *Pisaster brevispinus*).

MATERIALS and METHODS

A single lens reflex camera and a strobe light were used to stop the action of swimming gastropods. Motion pictures were obtained with a Super 8 Bauer C2A camera. Illustrations were made from various exposures.

The effectiveness of the motion picture camera has proven its worth. Rates of swimming or motion can be obtained from the known speed of the filmed animal. The shape of soft structures is recorded in different successive frames during the swimming motion.

In order to study the swimming of *Aplysia,* I filmed the 8 drawings in figure 22 of Pruvot-Fol (1954) and found that it appeared to be swimming backwards. This is not apparent from the illustrations. By reversing the drawings and filming, the animal appeared to be swimming forward (Figure 1).

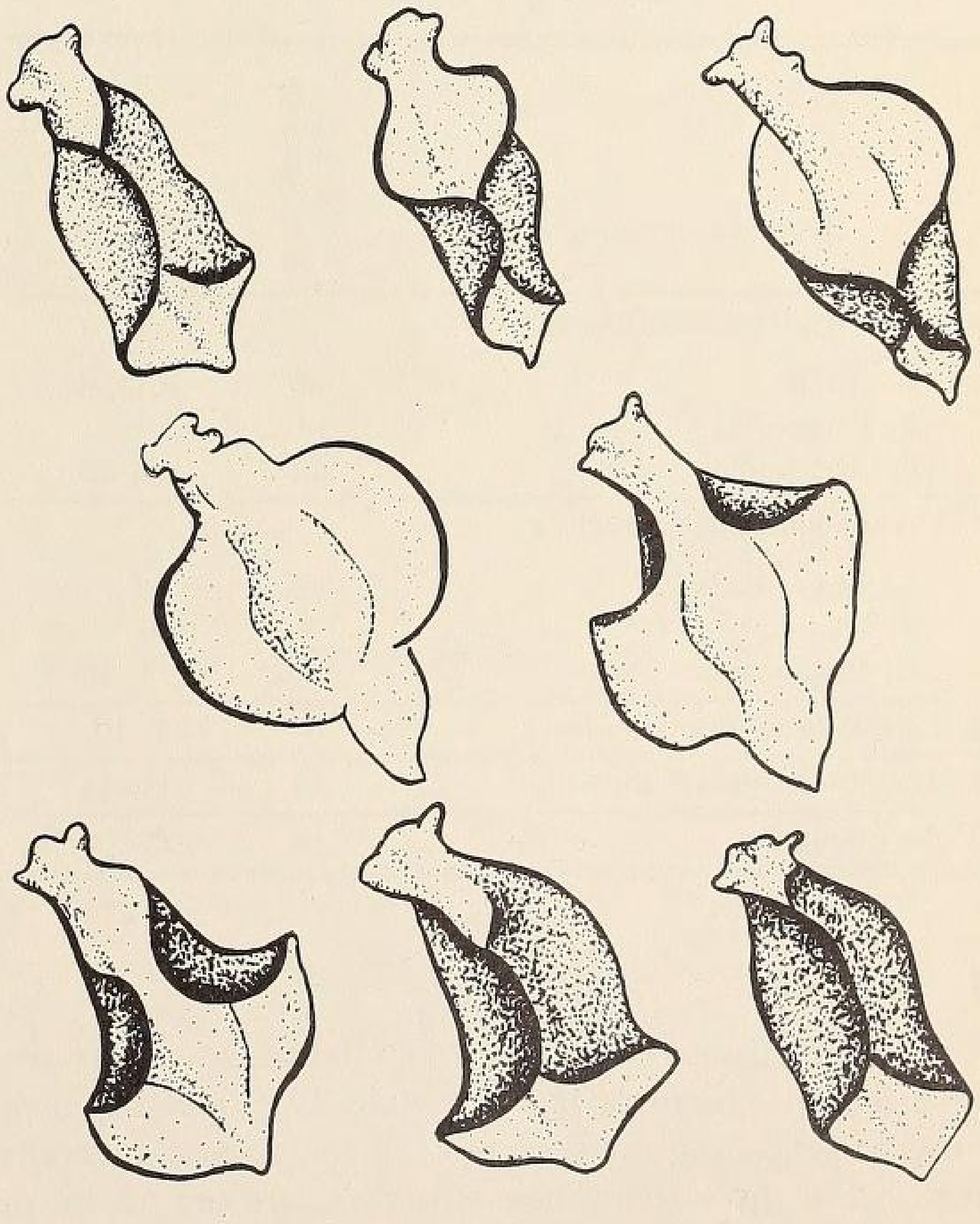


Figure 1

The swimming of *Aplysia* is redrawn from Pruvot-Fol, 1954, in proper sequence

There are several motion picture films of swimming opisthobranchs. Researchers as PRUVOT-FOL, TOKIOKA & BABA, RISBEC, THOMPSON & SLINN, MORTON & HOLME, HURST, HAEFELFINGER & KRESS have employed the motion picture film to obtain sequential drawings of the animal in the process of swimming. Figures 1, 16, 17 and 18 are from some of their reports and have been redrawn here to illustrate types of swimming.

SWIMMING GASTROPODS

The methods of swimming have been partially defined in the literature. For example: gastropods that "undulate" are many; however, the structure used and the method of undulating vary greatly. I will expand on and define some of the methods of swimming for various members of the opisthobranchs and prosobranchs. Pelagic forms, such as the pteropods and veligers, are not considered in this paper. Of the species included, the opisthobranchs outnumber the prosobranchs by 6 to 1.

Table 1

Swimming Classification

Type of Swimming	Table 2 abbreviations	Swimming example
1. Flapping structures (paired)		
A. Notal	nf	2, 3, 4
B. Parapodial	pf	1
C. Metapodial	mf	19, 20
2. Undulation (single structure)		
A. Entire body	ub	3
B. Foot	uf	16
C. Propodial	upro	17, 18
3. Lateral bending of the body	lb	5 - 10
4. The "breast stroke" movement	bs	11 - 15
5. Jet propulsion	jp	21

1. Flapping

Flapping through the water is interpreted as the use of 2 lateral structures that are waved up and down to provide propelling surfaces, moving the animal generally forward in the water. These structures are the notum or mantle, the parapodium and the metapodium.

A. Notal

The mantle edge of opisthobranchs has a progressive wave synchronous or asynchronous one side with the other.

B. Parapodial

Parapodial swimming is similar to notal swimming except that the structures fold over the top of the body when the animal is at rest. Its apparent initial thrust would be a downward stroke.

C. Metapodial

The metapodium of some prosobranchs is used to move the animal through the water. These flaps of tissue normally ride over the shell when the animal is crawling. When the animal swims, these structures move up and down at the sides. The metapodium arises ventrally. Metapodial swimming is similar to parapodial swimming.

2. Undulation

Undulation is defined as an up and down motion forming a progressive wave on the vertical plane through the body of the animal. The structure performing this is the propodium, the entire body, or just the foot. The animal may be upside down or right side up.

A. Entire body

In this method the dorsal surface and ventral surface provide the areas to push against the water and to move the animal forward. At least one dorid nudibranch uses this method of swimming.

B. Foot

Some prosobranchs use only the posterior $\frac{3}{4}$ of the foot which is "waved" for propulsion through the water. The anterior part of the foot is apparently of little use.

C. Propodium

The propodium of some prosobranchs is used to great advantage in propelling the animal through the water. In this case the anterior part of the animal is used in swimming, while the posterior part merely trails. Motion of the propodium is up and down.

3. Lateral bending of the body

By far more nudibranchs fall into this category than into any other. The head and tail rapidly approach each other, first on one side and then on the other. This process is repeated for some time with the flattened sides providing the propelling surfaces. Usually the animal moves upward with either the foot or back uppermost.

Table 2

Swimming Opisthobranchs and Prosobranchs
(see Table 1 for explanation of abbreviations under swimming types)

	Swimming Type	Reference
CEPHALASPIDEA		
PHILINACEA		
GASTROPTERIDAE		
Gastropteron bicornutum BABA & TOKIOKA, 1965	pf	BABA & TOKIOKA, 1965
Gastropteron cinereum DALL, 1925	?	TOKIOKA & BABA, 1964
Gastropteron flavum TOKIOKA & BABA, 1965	pf	BABA & TOKIOKA, 1965
Gastropteron fuscum BABA & TOKIOKA, 1965	pf	BABA & TOKIOKA, 1965
Gastropteron japonicum TOKIOKA & BABA, 1965	?	TOKIOKA & BABA, 1964
Gastropteron pacificum BERGH, 1893	pf	BERTSCH, 1969
Gastropteron rubrum (RAFINESQUE, 1814)	pf	HAEFELFINGER & KRESS, 1967a
Gastropteron sibogae BERGH, 1905	?	TOKIOKA & BABA, 1964
Gastropteron sinensis A. ADAMS, 1861	pf	TOKIOKA & BABA, 1964
Gastropteron viride TOKIOKA & BABA, 1964	?	TOKIOKA & BABA, 1964
Sagaminopteron ornatum TOKIOKA & BABA, 1964	pf	TOKIOKA & BABA, 1964
ASCOGLOSSA		
ELYSIACEA		
ELYSIIDAE		
Elysia pilosa RISBEC, 1928	pf	RISBEC, 1928
ANASPIDEA		
APLYSIACEA		
AKERATIDAE		
Akera O. F. MÜLLER, 1776		MORTON, 1967
Akera bullata O. F. MÜLLER, 1776	pf	HAEFELFINGER & KRESS, 1967b
APLYSIIDAE		
Aplysia LINNAEUS, 1767		PRUVOT-FOL, 1954
Aplysia depilans GMELIN, 1791	pf	HAEFELFINGER & KRESS, 1967b
Aplysia fasciata Poiret, 1789	pf	HAEFELFINGER & KRESS, 1967b
Aplysia punctata CUVIER, 1803	pf	HAEFELFINGER & KRESS, 1967b
Notarchus CUVIER, 1817		PRUVOT-FOL, 1954
Notarchus punctatus PHILIPPI, 1836	jp	HAEFELFINGER & KRESS, 1967b
NOTASPIDEA		
PLEUROBRANCHACEA		
PLEUROBRANCHIDAE		
Pleurobranchus (membranaceus) tuberculatus MECKEL, 1808	nf	THOMPSON & SLINN, 1959
Oscanius tuberculatus MECKEL, 1808	nf	MARTIN, 1966
Euselenops luniceps (PACE, 1901)	nf	PELSENEER, 1935
NUDIBRANCHIA		
Doridoidea		
Cryptobranchia		
HEXABRANCHIDAE		
Hexabranchus aureomarginatus OSTERGAARD, 1955	nf	NEU, 1932
Hexabranchus imperialis, possibly *H. marginalis*	nf	HAEFELFINGER & KRESS, 1967b
Hexabranchus marginatus QUOY & GAIMARD, 1833	ub, nf	EDMUNDS, 1968 RISBEC, 1928 VICENTE, 1963
Hexabranchus tinkeri OSTERGAARD, 1955	nf	OSTERGAARD, 1955
Hexabranchus sanguineus (RÜPPELL & LEUCKART)	nf	GOHAR & SOLIMAN, 1963
Phanerobranchia		
NONSUCTORIA		
POLYCERIDAE		
Nembrotha eliora MARCUS, 1967	lb	LANCE, 1968
Plocamopherus F. S. LEUCKART, 1828		PRUVOT-FOL, 1954
Triopa fulgurans RISBEC, 1928	lb	RISBEC, 1925

Table 2 [continued]

	Swimming Type	Reference
DORIDIDAE		
Archidoris nubilosa	nf	KAY, pers. comm.
Goniodoridinae		
Trapania velox (COCKERELL, 1901)	lb	COCKERELL, 1901
DENDRONOTACEA		
DENDRONOTIDAE		
Dendronotus giganteus O'DONOGHUE, 1921	lb	HAEFELFINGER & KRESS, 1967b
Dendronotus iris COOPER, 1863	lb	BERTSCH, pers. comm.
Dendronotus nanus MARCUS, 1967	lb	MARCUS, 1967
Dendronotus albus MACFARLAND, 1966	lb	LONG, pers. comm.
Dendronotus frondosus (ASCANIUS, 1774)	lb	LONG, pers. comm.
Dendronotus subramosus MACFARLAND, 1966	lb	LONG, pers. comm.
BORNELLIDAE		
Bornella (GRAY) ADAMS & REEVE, 1848		RISBEC, 1928
Bornella digitata RISBEC, 1953	lb	RISBEC, 1953
SCYLLAEIDAE		
Scyllaea pelagica (LINNAEUS, 1758)	lb	PRUVOT-FOL, 1954
TRITONIIDAE		
Melibe leonina (GOULD, 1852)	lb	HURST, 1968
Melibe pilosa PEASE,	lb	
Chioraera dalli HEATH, 1917	lb	HEATH, 1917
Fimbria fimbria (BOHADSCH, 1761)	lb	PRUVOT-FOL, 1954
Marionia tethydes DELLE CHIAJE, 1828	lb	HAEFELFINGER & KRESS, 1967b
AEOLIDOIDEA		
Pleuroprocta		
FLABELLINIDAE		
Coryphella (Flabellinopsis) iodinea (COOPER, 1862)	lb	MACFARLAND, 1966
Coryphella cynara MARCUS, 1967	bs	MARCUS, 1967
Flabellina telja MARCUS, 1967	lb	MARCUS, 1967
PHYLLOBRANCHILLIDAE		
Phyllobranchillus orientalis KELAART, 1858	bs	RISBEC, 1953
Eolidoidea		
AEOLIDIIDAE		
Aeolidiella alba RISBEC, 1928	bs	PRUVOT-FOL, 1954
ARCHAEOGASTROPODA		
TROCHACEA		
TROCHIDAE		
Solariella nektonica OKUTANI, 1961	uf	OKUTANI, 1961
MESOGASTROPODA		
VIVIPARACEA		
AMPULLARIIDAE		
Ampullarius	upro	PELSENEER, 1935
NATICACEA		
NATICIDAE		
Polinices josephinus (RISSO, 1838)	upro	ZIEGELMEIER, 1958
NEOGASTROPODA		
Stenoglossa		
VOLUTACEA		
OLIVIDAE		
Olivella biplicata (SOWERBY, 1825)	mf	EDWARDS, 1969
Olivella zanoeta (DUCLOS, 1835)	mf	
Olivella verreauxii (DUCROS, 1857)	mf	WILSON, 1969
Oliva tehuelchana (D'ORBIGNY, 1841)	mf	WILSON, 1969
Ancillista cingulata (SOWERBY, 1830)	upro	WILSON, 1969

4. The "breast stroke" movement

As the human swimmer uses his extremities, these nudibranchs use their cerata to "stroke" the water, rowing themselves into the water column. The animal moves forward.

5. Jet propulsion

Water is taken into the peribranchial cavity formed by the joined parapodia, and forced out through a small opening, causing the animal to move in the opposite direction.

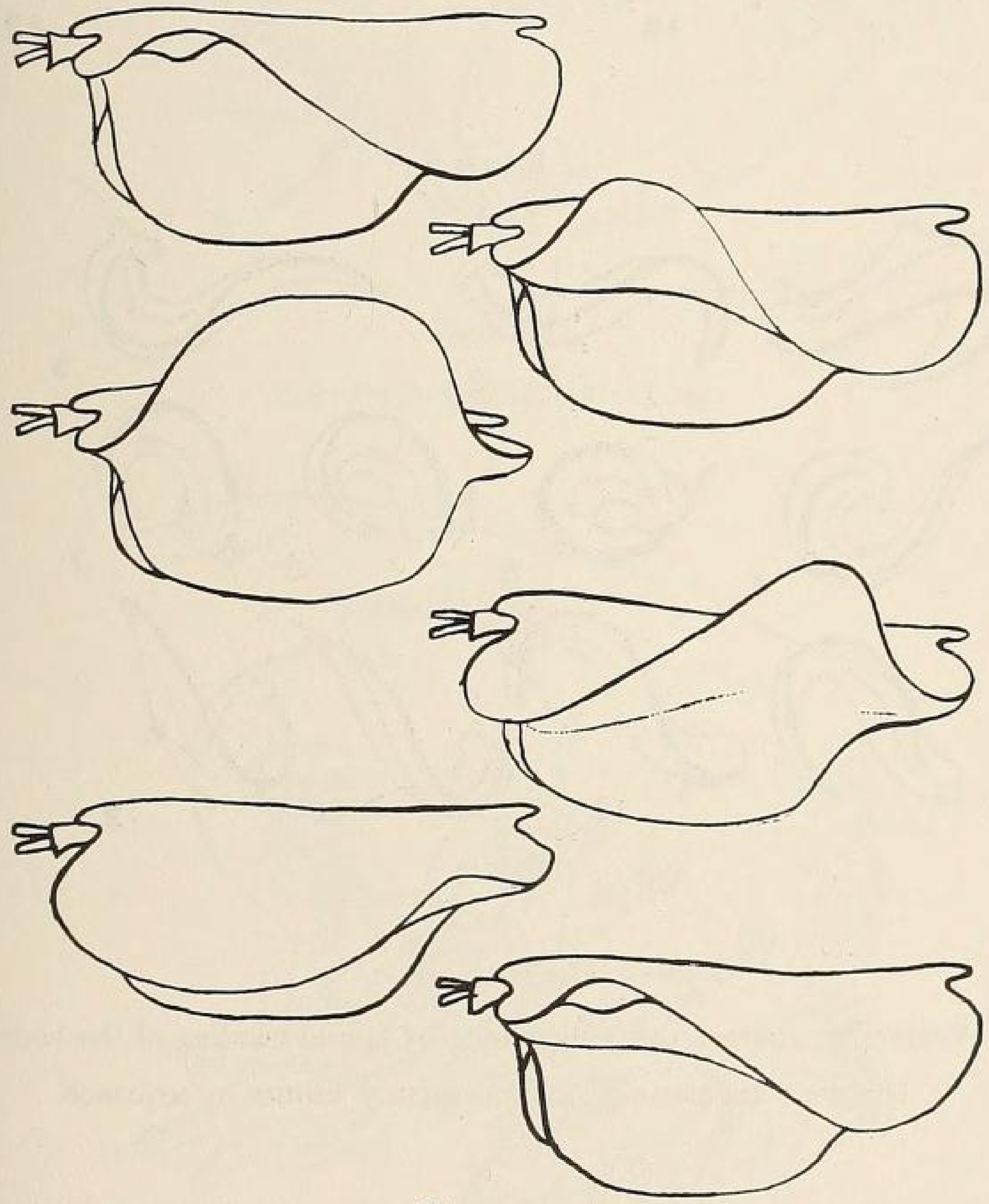


Figure 2

The swimming of *Pleurobranchus tuberculatus* after THOMPSON & SLINN, 1959

SWIMMING OPISTHOBRANCHS

Swimming by opisthobranchs has been well documented by earlier investigators. Many of the early observations concerned the manner an opisthobranch used as a means of locomotion. More recently, RISBEC, PRUVOT-FOL, THOMPSON & SLINN, HAEFELFINGER & KRESS, BABA, TOKIOKA, MARTIN, EDMUNDS, HURST, CRAIG, WILSON & VICENTE have given excellent descriptions, with illustrations, of the manner of swimming which the animal exhibited.

There are 47 species listed in Table 2, that have been reported as having the ability to swim. Much of the classification follows TAYLOR & SOHL (1962).

Information as to the rate of swimming is scattered. Comparisons with other opisthobranchs can be found in Table 3. The size of animals with swimming locomotion ranges from a few millimeters in *Gastropteron* to over 40 cm in *Aplysia*.

Dr. George E. Radwin (personal communication) observed several hundred aplysids (propably *Aplysia dactylomela* RANGE, 1828) swimming near the surface under night lights in Florida. Dr. Alison Kay (personal communication) has reported seeing *Hexabranchus tinkeri, H. aureomarginatus* and *Archidoris nubilosa* swim. OSTERGAARD (1955) says of the Hexabranchids "Swimming is effected by vigorous transverse flextions [sic] of the body and undulating movements of the broad, thin cloak, which serves as fins" (Figures 3, 4).

COCKERELL (1901) says of *Thecacera velox* (now *Trapania velox*) "... very active when swimming with an undulating motion at the surface of the water." I worked with this species and tried unsuccessfully to induce it to swim.

By far a majority of swimming species apparently use lateral bending of the body as an auxiliary method of locomotion (Figures 5 - 10). Of the Nudibranchia, most members of the suborders Eolidoidea and Dendronotoidea employ this method. A few limaciform members of the suborder Doridoidea also use this method of swim-

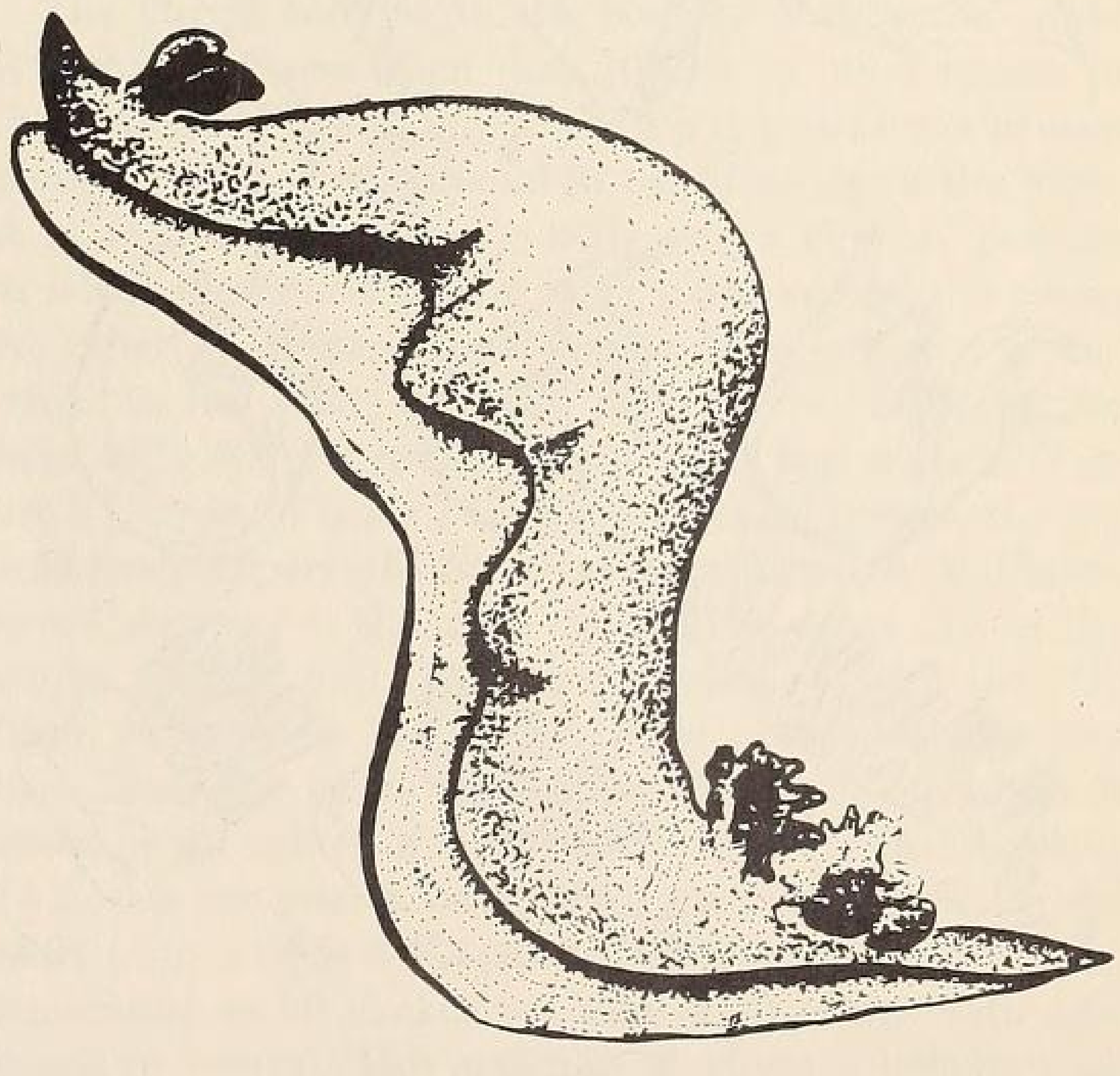


Figure 3

Hexabranchus marginatus in the process of swimming redrawn from EDMUNDS, 1968

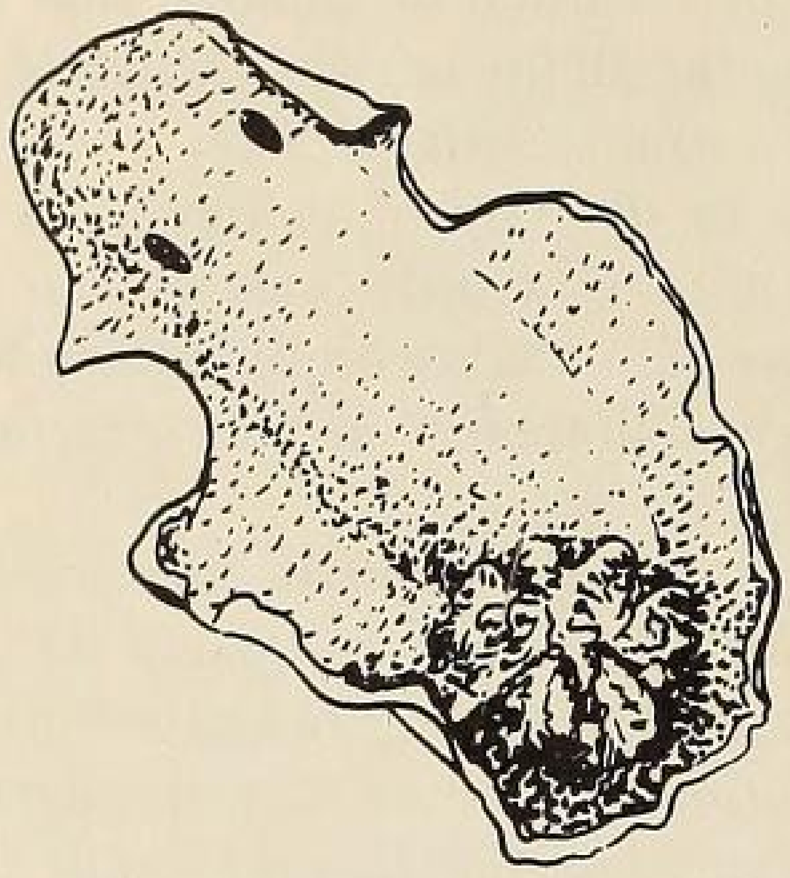


Figure 4

Hexabranchus sanguineus swimming. Redrawn from Gohar & Soliman, 1963

ming, *i. e., Nembrotha eliora* (Figures 6, 7), a nonsuctorian nudibranch.

Heath (1917) says of *Melibe leonina* "... body is strongly flexed from side to side." MacFarland (1966)

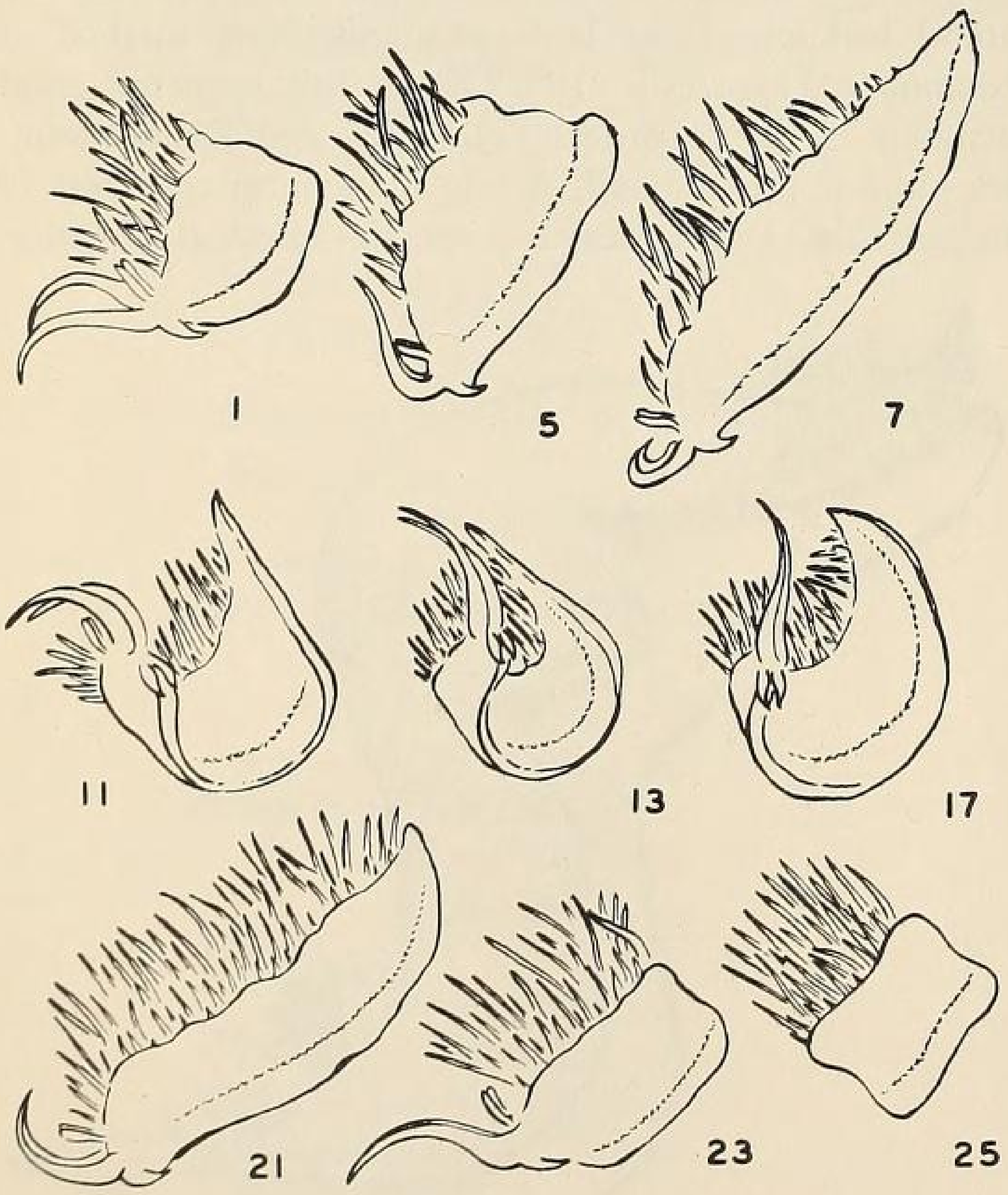


Figure 5

Coryphella iodinea swimming by lateral bending of the body. Numbers are those of motion picture frames in sequence.

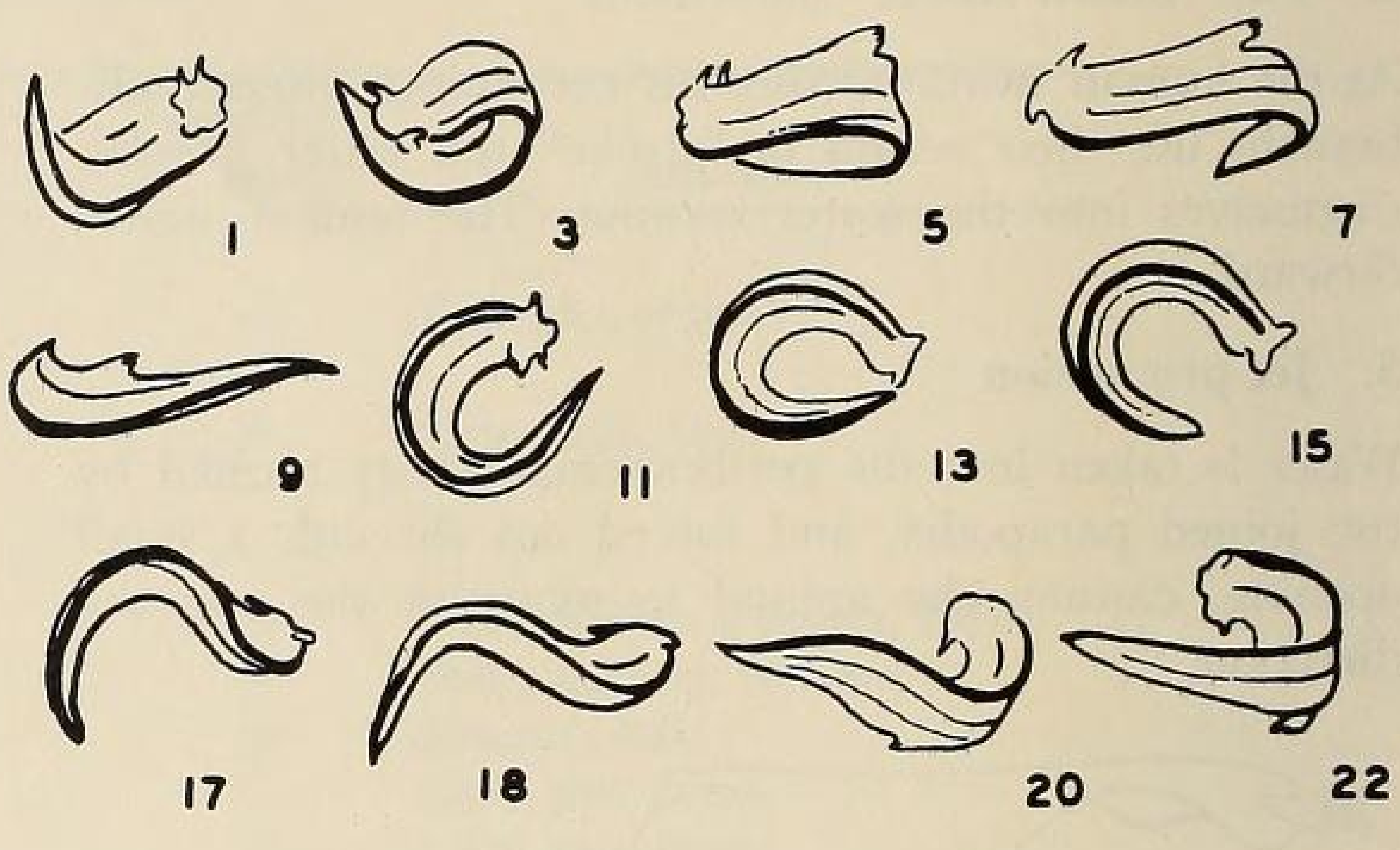


Figure 6

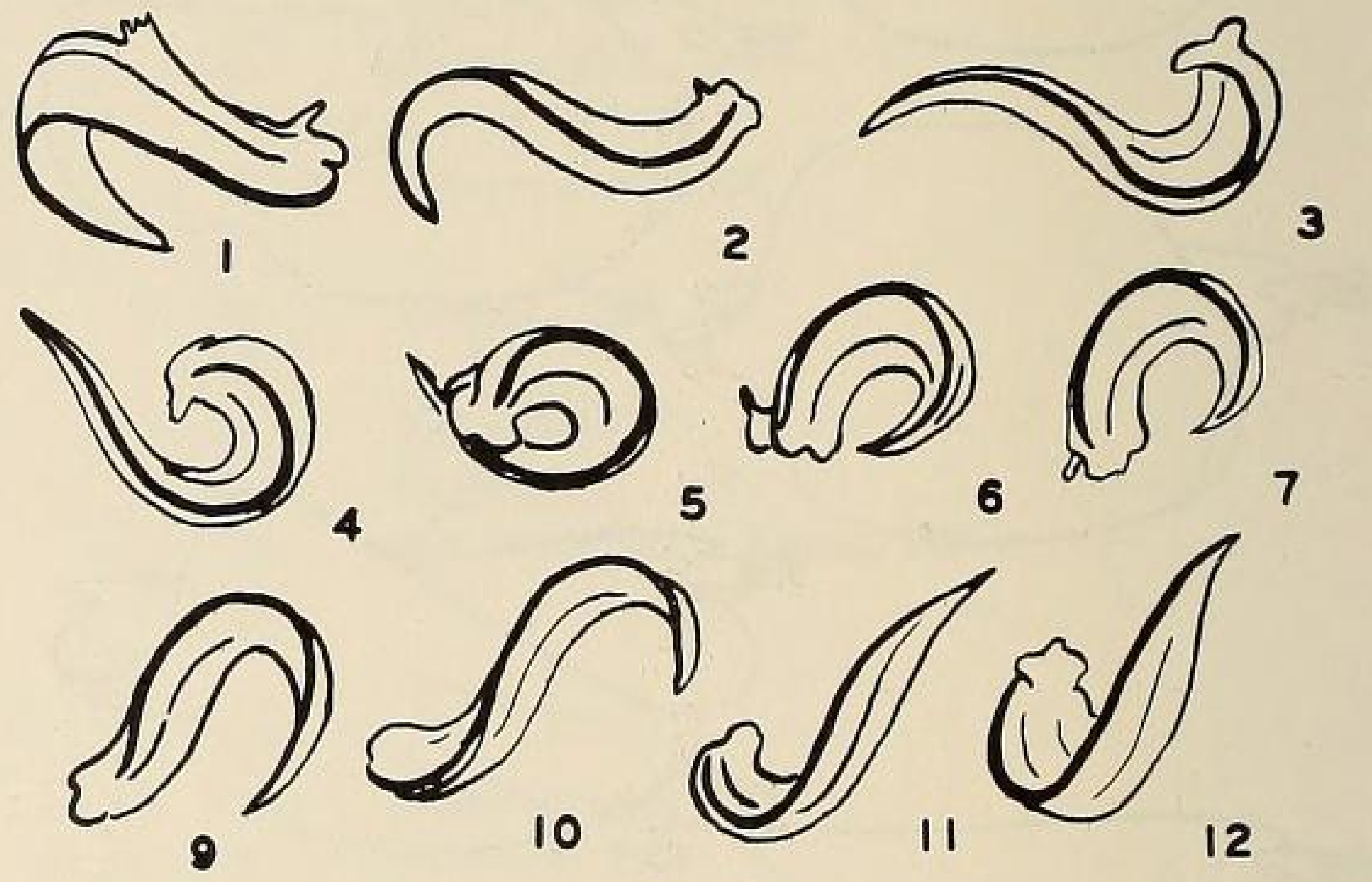


Figure 7

Figures 6 and 7

Nembrotha eliora actively swimming by lateral bending of the body. Numbers are those of motion picture frames in sequence.

says of *Coryphella iodinea* "... swims freely by doubling the body laterally from side to side until head and tail meet ..." A good example of this is seen in Figure 5. Lance (1968) reported *Nembrotha* "... swimming ... by undulating its body from side to side ..."

Hurst (1968) writes "*Melibe leonina* just prior to swimming folds the whole foot longitudinally so that the right and left halves of the sole meet. The body becomes laterally compressed while the dorsal papillae elongate and flatten. In this manner the animal presents maximal surface area for swimming." Hurst reports that the rate and degree of bending determine the speed of progress. The hood of *Melibe* plays no major part in propulsion. Hurst stresses that the animal swims upside down.

A slight variation of the usual method was reported by

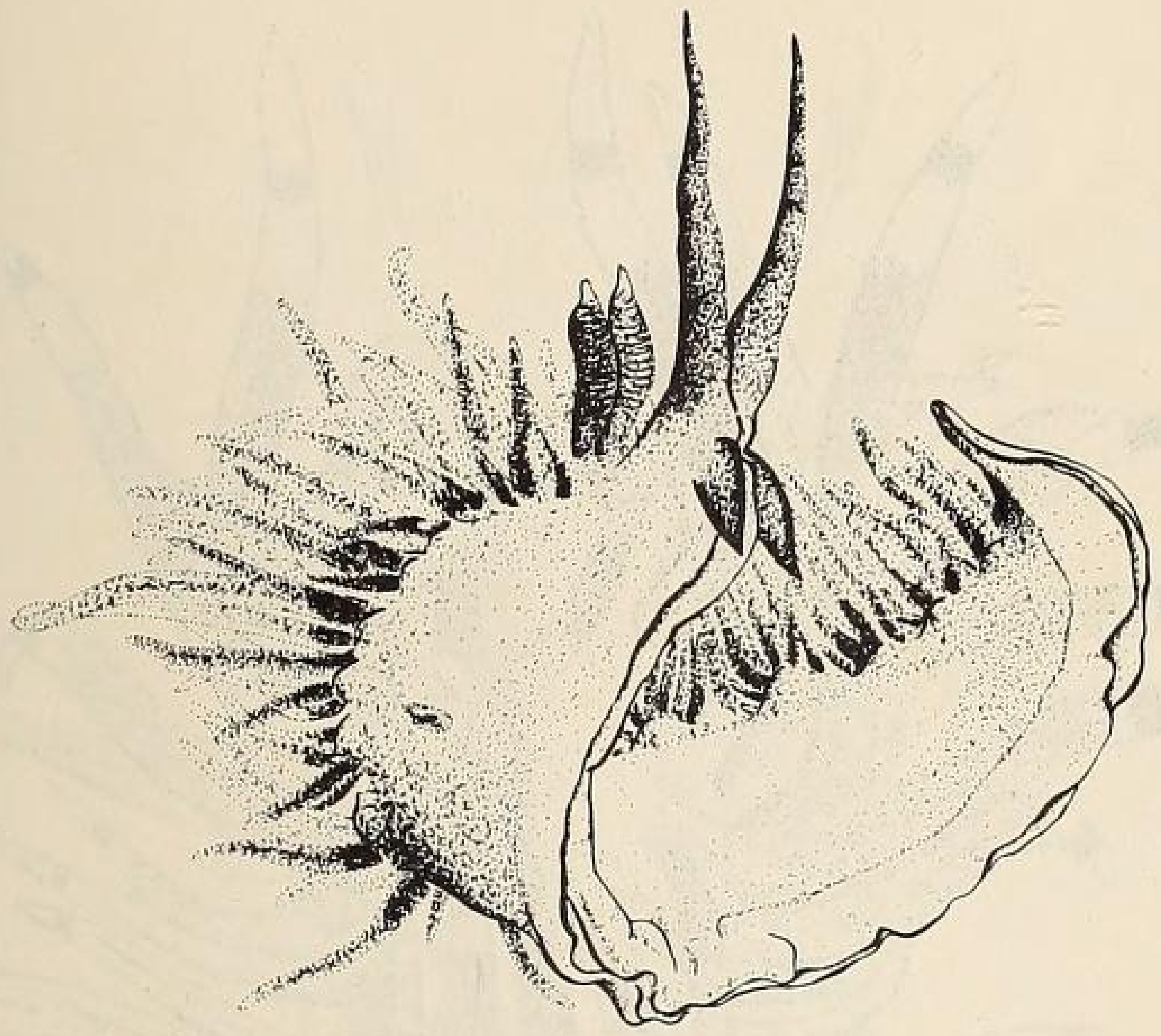


Figure 8

Coryphella iodinea swimming

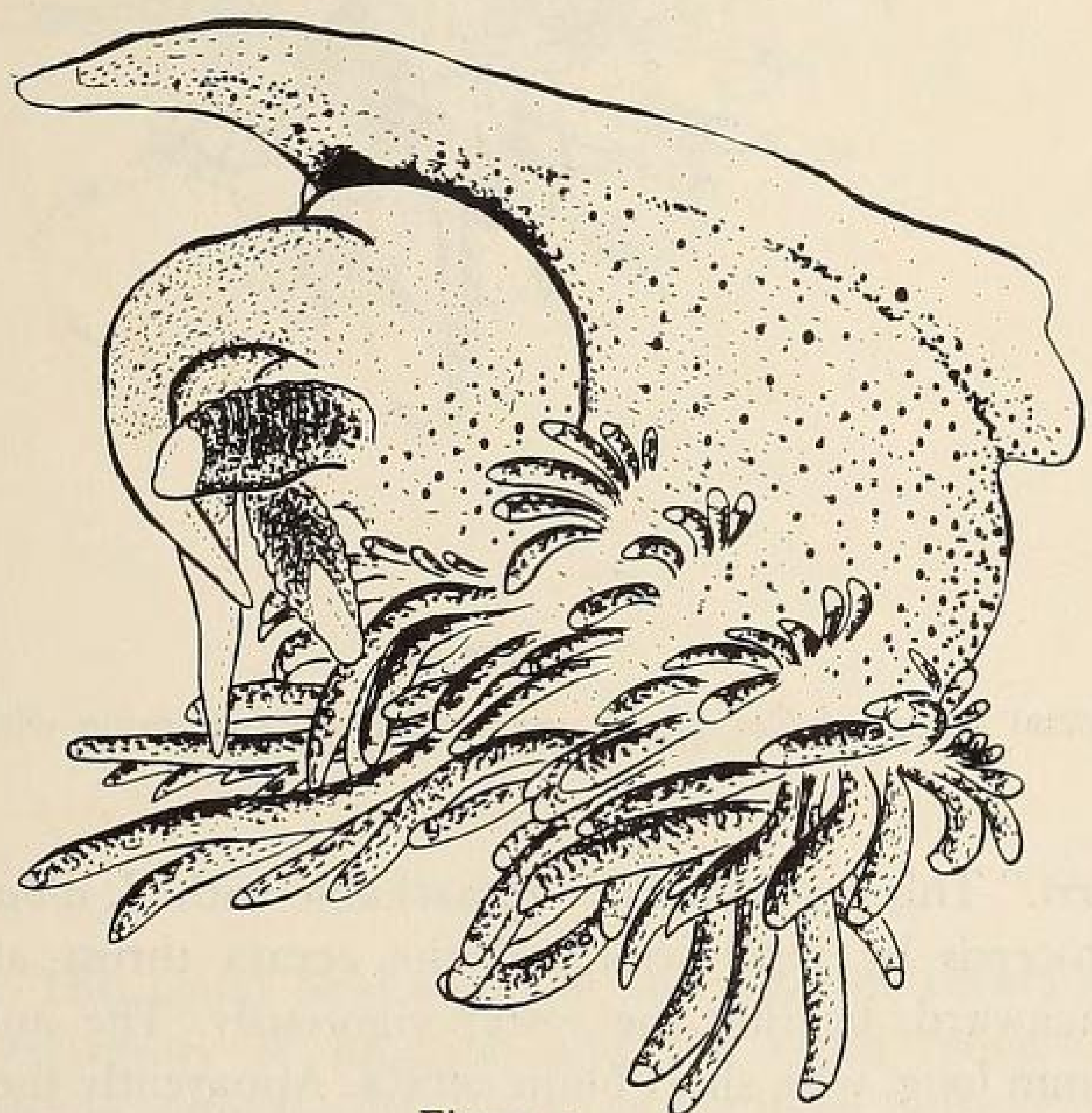


Figure 9

Flabellina telja swimming by lateral bending of the body

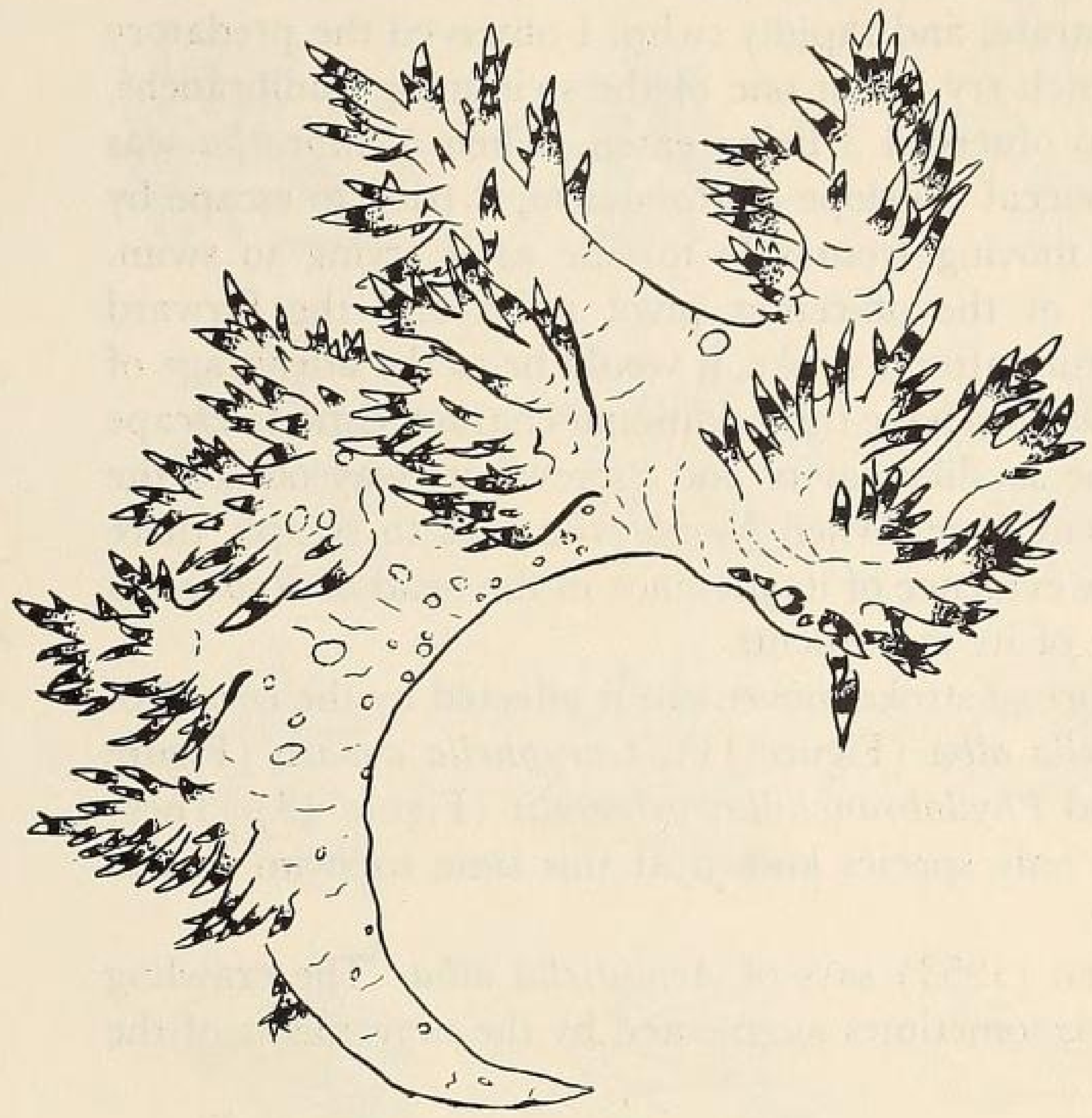


Figure 10

Dendronotus nanus swimming by lateral bending of the body

Agersborg (1923) for *Dendronotus giganteus.* "It swims by bending the anterior end of the body sideways, forming a wave-like twist in the side of the body wall like that in a blade of a propeller. This wave passes gradually toward the posterior end and disappears when the animal makes the next stroke to the opposite side. When the animal makes a stroke to the right the posterior two thirds is bent so as to form an angle of 45° with the anterior one third. But the posterior part of the body also rotates about 45° from the vertical plane, so that the left side with the foot forms a large wave which sweeps posteriorly, while the anterior part of the body, in front of the wave, is kept vertical."

The lateral bending of the body in *Nembrotha eliora* is slightly different from that utilized by other species in this method of swimming. There is a degree of momentum along the axis of the animal in the direction of the head. A rapid flexing brings the body into a circular position at which continued motion takes place around the circle. At times when the animal passes from one side of the stroke to the other, the body takes on an "S" form, the head initiating the stroke while the tail lags slightly (Figure 6 [18] and Figure 7 [2, 10]). In other species, the tail and head apparently travel at approximately the same speed, meeting at the same time on the other side of the stroke (Figure 5 [13]), without going through the "S" form. *Nembrotha* has a pivot point about $\frac{3}{4}$ of the way back from the head, while the pivot point on others is about at the center of the body. *Nembrotha* makes about $1\frac{1}{2}$ strokes per second. At 18 frames per second the animal went from a tight coil to the other side and back again, amounting to 90 strokes per minute. It swims with foot dorsal or ventral. This action in *N. eliora* is definitely an escape response, for when this species comes in contact with the predacious nudibranch (which, for now, will be called *Roboastra* sp.), there is an immediate reaction to move the head away with a fast jerk, free its hold on the substrate, and rapidly swim. I observed the predatory nudibranch try to eat one of the swimming nudibranchs, and also observed 3 being eaten. When *Nembrotha* was in the buccal envelope of *Roboastra,* it tried to escape by rapidly moving from side to side as if trying to swim. Because of the off-center pivot point and the forward momentum after a stroke, it would be to the advantage of *Nembrotha* to have this additional characteristic to escape from the sac-like cavity and "screw" its way out of the buccal envelope. When *Nembrotha* fails to escape, there is visible evidence of its presence in the head of *Roboastra* because of its movements.

The breast stroke movement is effected by the cerata of *Aeolidiella alba* (Figure 11), *Coryphella cynara* (Figure 12), and *Phyllobranchillus orientalis* (Figure 13). These are the only species known at this time to swim in this manner.

Risbec (1953) says of *Aeolidiella alba* "The crawling motion is sometimes augmented by the movements of the

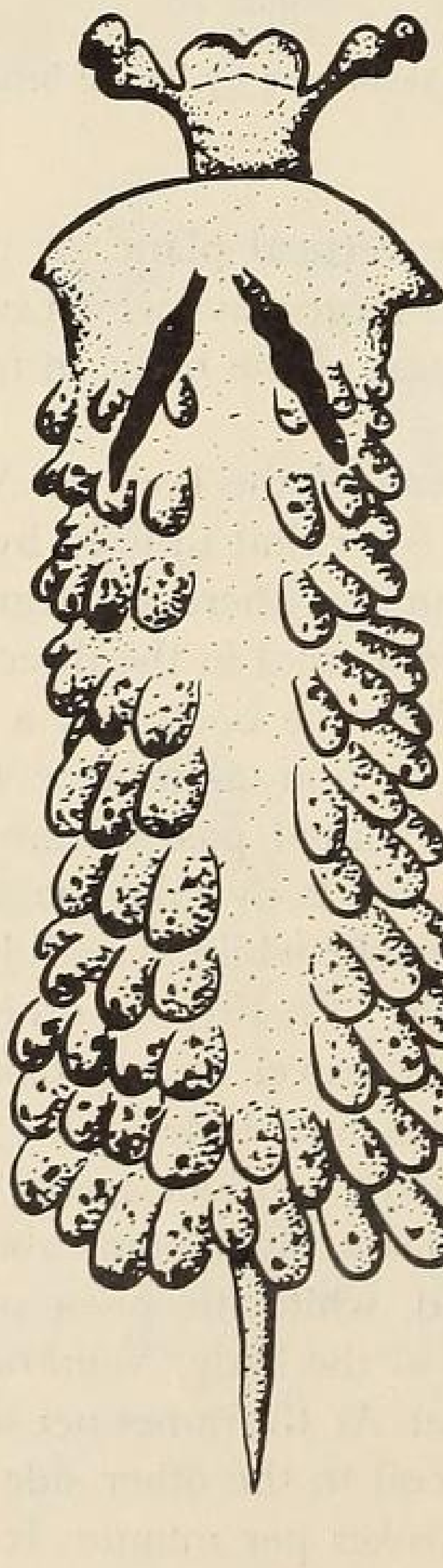


Figure 11

Aeolidiella alba. Cerata are used by this species for swimming, after Risbec, 1953

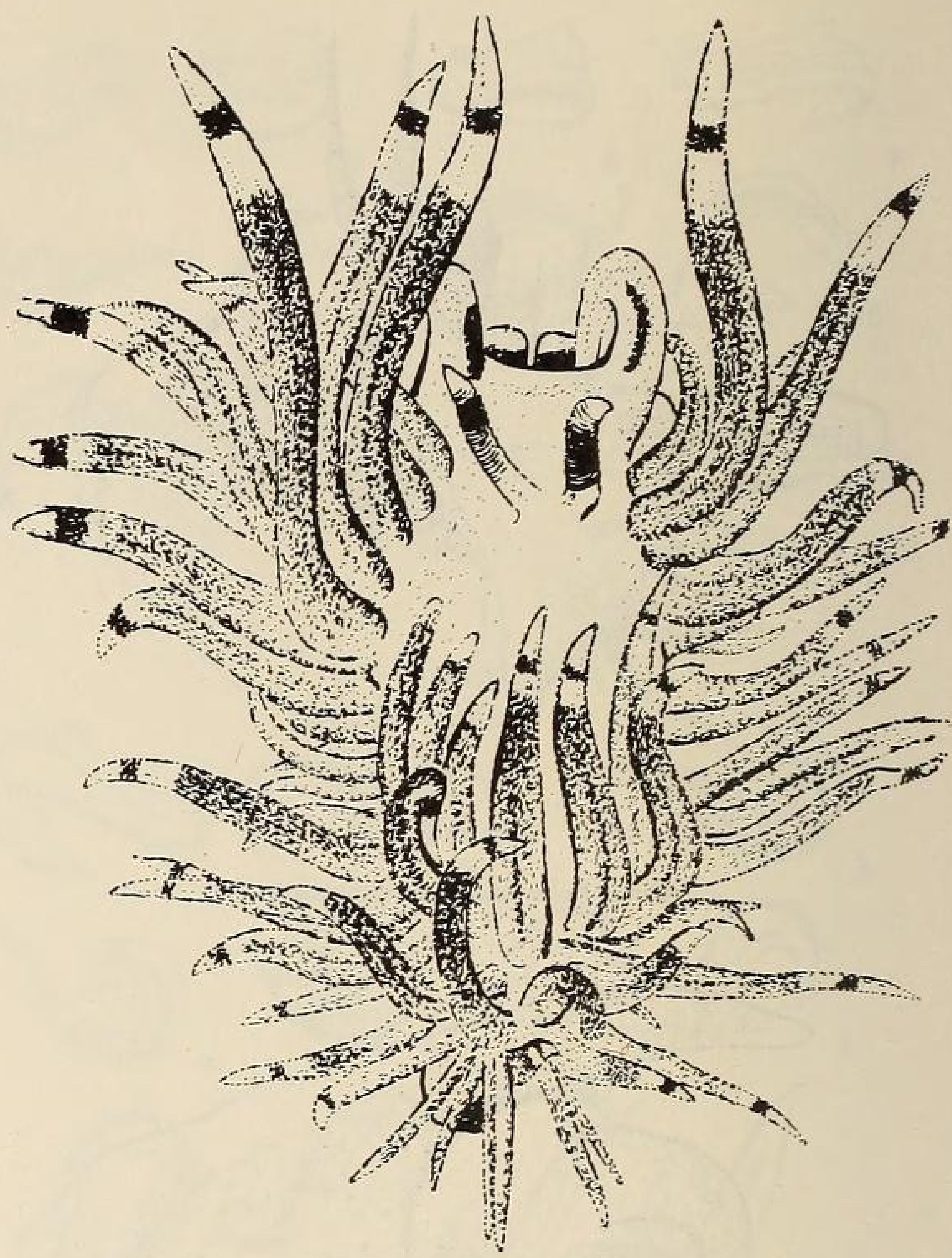


Figure 12

Dorsal aspect of *Coryphella cynara* actively swimming with cerata

cirri." This is particularly remarkable with *A. alba* which proceeds by jerks while all the cerata thrust abruptly backward, beating the water vigorously. The animal is 6 mm long, with short blunt cerata. Apparently the swimming motion augments the crawling and is probably a combination of swimming and crawling.

Risbec (1928) says of *Phyllobranchillus orientalis* "The papillae of it are, in fact, very motile and serve for locomotion." The animal is about 4 cm in length. Risbec (1953) figures and discusses the animal further (see Figure 13).

Coryphella cynara has only recently been recognized as a swimmer. It has great strength and stamina when it swims and can remain in the water column for periods greater than 45 minutes without noticeably resting. There is apparently a lack of fatigue in the muscles moving the

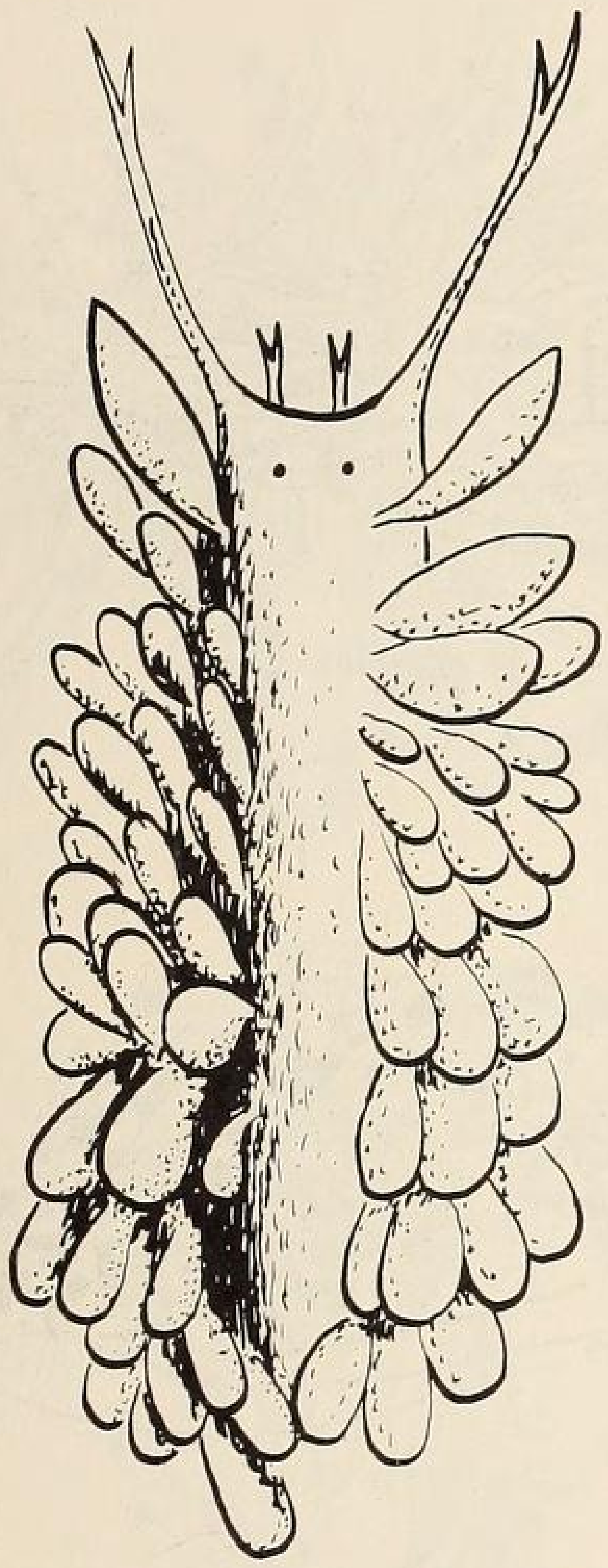


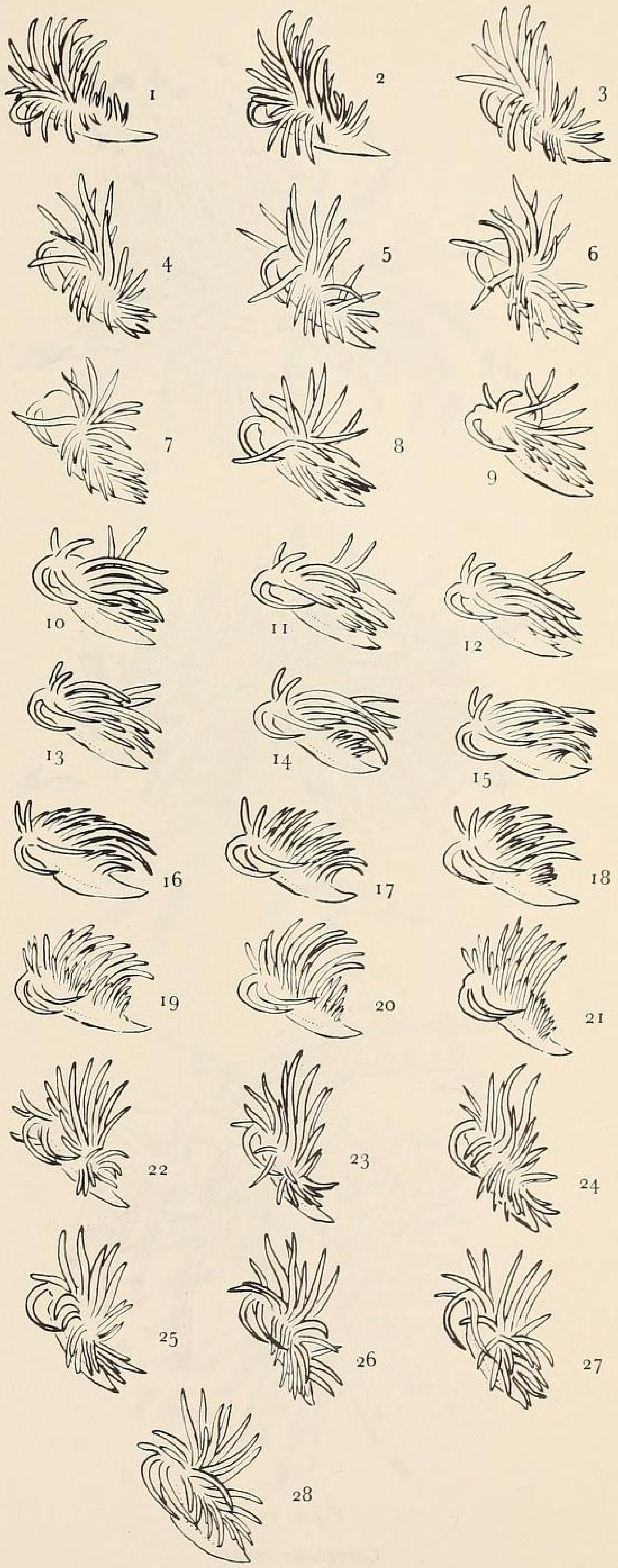
Figure 13
Phyllobranchillus orientalis swims with cerata, after RISBEC, 1953

cerata. This could be due to the fact that the cerata are also respiratory in function and the rapid movement through the water hyper-oxygenates the inner fluids which bathe the muscles, removing fatigue-producing by-products.

The species lives in the upper Gulf of California and apparently is an occasional visitor to the shallow water from deeper areas. *Coryphella cynara* is a carnivore and has been observed eating *Hermissenda crassicornis* in captivity (Lance, pers. comm.). Because it ventures into the

(adjacent column ⟶)

Figure 14
Sequence of *Coryphella cynara* swimming



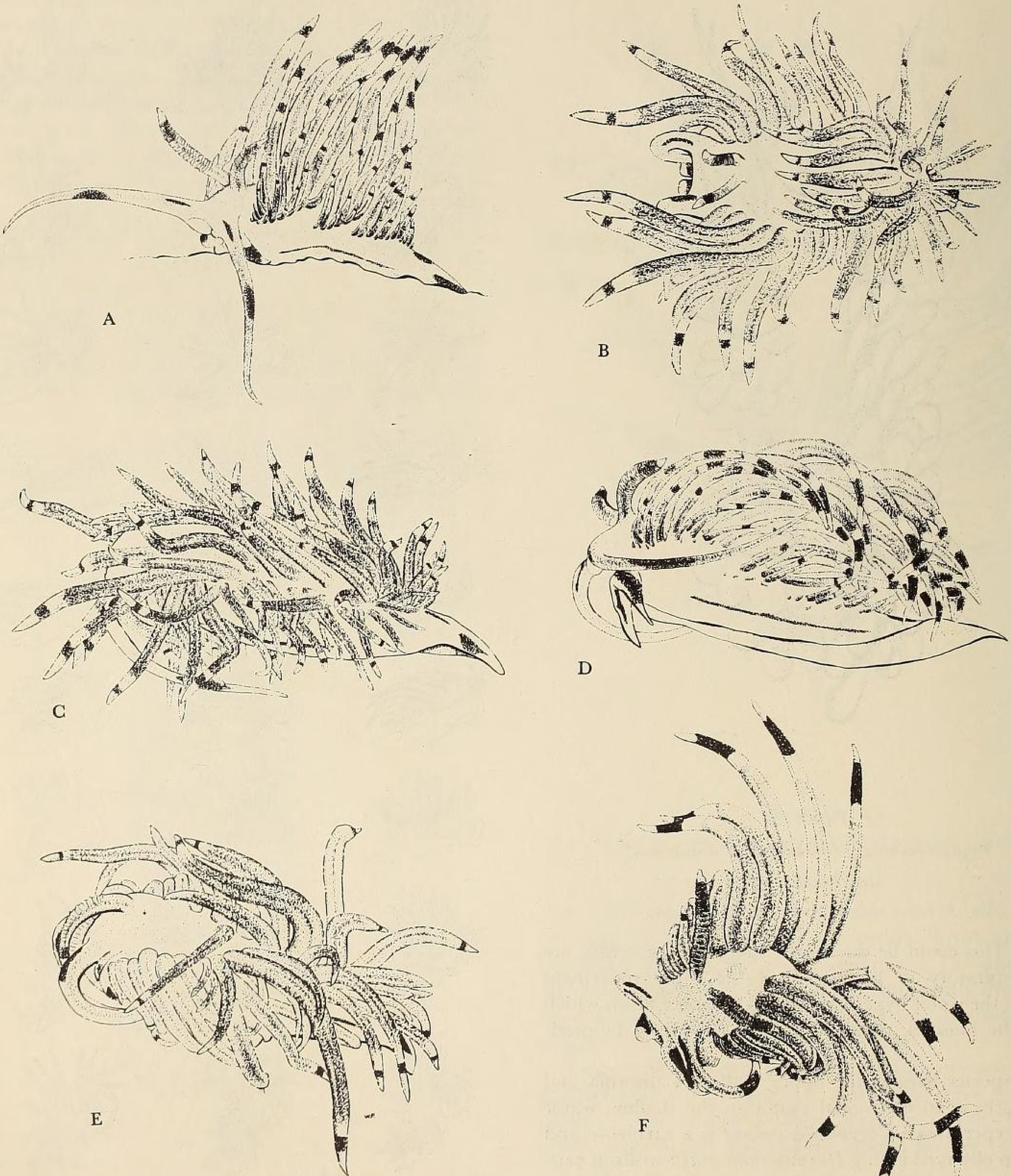
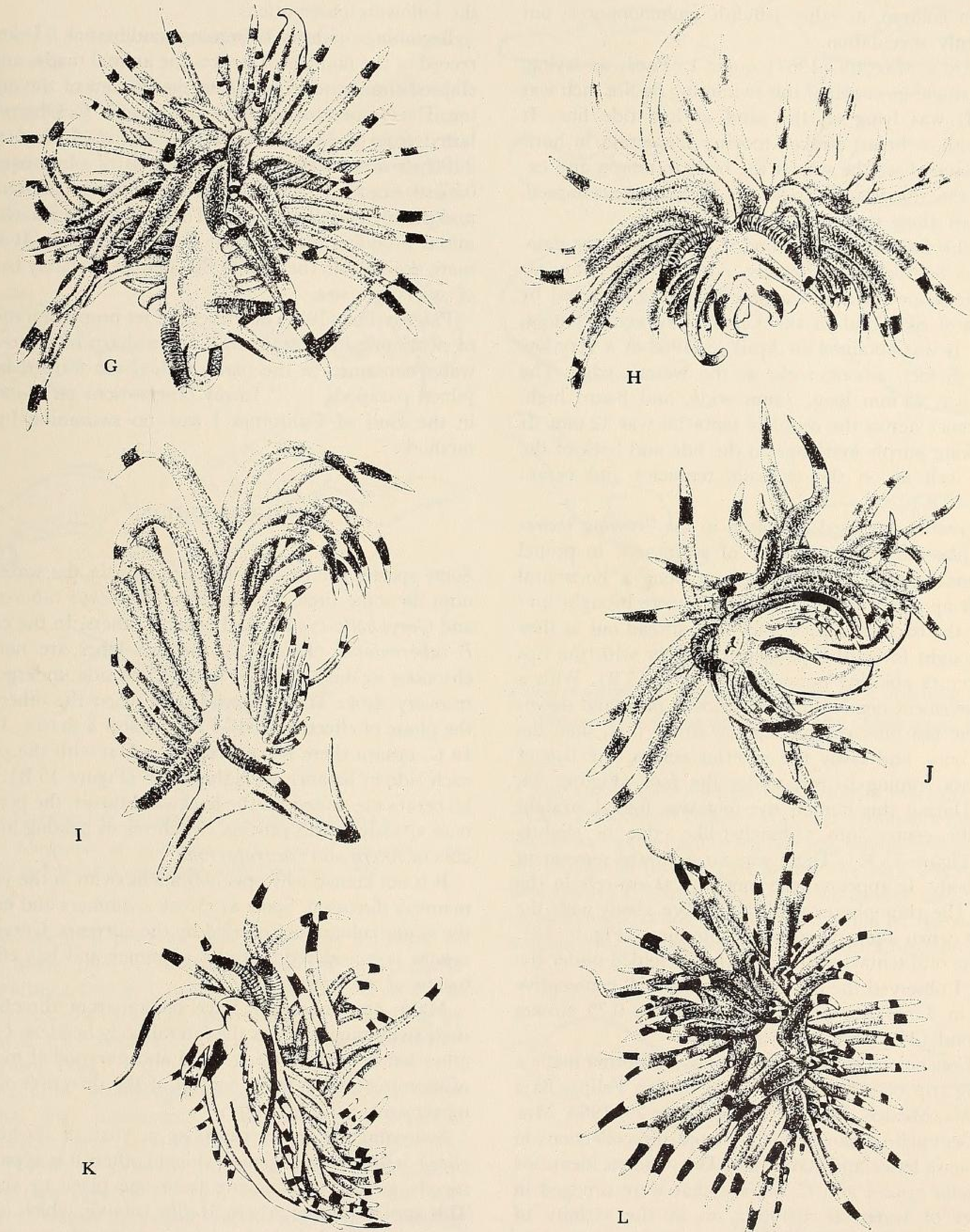


Figure 15

Coryphella cynara

A: actively crawling – B to L: actively swimming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upper water it may feed to a great extent on organisms in the water column, as salps, jellyfish, siphonophores; but this is only speculation.

MARCUS & MARCUS (1967) quote L. Pardy as saying, "Only a single specimen of this swimming nudibranch was found. It was lying on the sand at low tide line. It swims with a 'breast stroke', moving the cerata in horizontal plane along the side of the body in unison and extended. On the return stroke the cerata are collapsed, but return along the same plane."

With this first account in mind, I will expand the data. Mrs. Eva Schroeder of Phoenix, Arizona, called my attention to a specimen of *Coryphella cynara* collected by Mrs. Carol Skoglund in the Cholla Bay area, Sonora, Mexico. It was obtained on April 13, 1968 at a very low tide of -6 feet, among rocks at the water's edge. The animal was 25 mm long, 7 mm wide, and 8 mm high. The distance across the cephalic tentacles was 32 mm. It had striking purple markings on the side and back of the foot as well as on the cephalic tentacles and cerata (Figure 15 A).

The cerata were used in unison in the "rowing movement," like the "breast stroke" of swimmers, to propel the animal upward and forward or along a horizontal plane. It appeared that all the cerata were brought into play for the backward stroke, for they spread out as they were brought forward in a bowed manner with the tips of the cerata pointing posteriorly (Figure 15 B). With a swift movement nearly all cerata moved back and downward, the last ones completing the stroke first, then the middle ones, and lastly the anterior cerata, the tips of the cerata coming to rest under the foot (Figures 14, 15 F). During this motion the foot was folded straight down the center into a hatchet-like edge or slightly apart (Figure 15 K). There was no sideward movement of the body. It appeared the motion was entirely in the cerata. The rhinophores tended to move about with the currents when the animal was swimming (Figure 15), while the oral tentacles were apparently folded under the animal. I observed the animal swimming 150 consecutive strokes in 3 minutes 21 seconds, or about 0.75 strokes per second (44.1 strokes per minute).

The Conchological Club of Southern California made a dredging trip on a shrimp boat out of San Felipe, Baja California, Mexico, June 27 through June 29, 1968. Mrs. Joyce Gemmell of San Felipe reported the collections in a club news letter and stated that Don Cadien identified *Coryphella cynara* and *C. iodinea* that were dredged in 126 feet of water at 10:30 a. m. in the vicinity of Consag Rock off San Felipe. Two specimens were given to Mr. J. R. Lance. A 28 mm long specimen was less strikingly colored than the specimen from Cholla Bay. Later, with the animal in a one-gallon aquarium, I made the following observations.

Beginning with a swimming nudibranch, I kept a record of the number of strokes the animal made, and the elapsed time until it settled to the bottom of the aquarium. The temperature of the water was 26° C. Observation lasted from 1:17 p. m to 2:02:30 p. m. It had swum 2 100 strokes during the 45½ minutes of observation or 0.77 strokes per second. It began swimming again at 2:18 and stopped at 2:45 p. m. The animal swam without initial prodding and without touching bottom. It swam more slowly than the Cholla Bay animal probably because of its larger size.

PRUVOT-FOL (1954) describes the jet propulsion method of swimming for *Notarchus* " ... a sharp recoil to expel water contained in the peribranchial sac formed by the joined parapods ... " In my observations on *Notarchus* in the Gulf of California I saw no swimming by this method.

DISCUSSION

Some species are capable of remaining in the water column for some time, such as *Pleurobranchus tuberculatus* and *Coryphella cynara*, and possibly others. In the case of *P. tuberculatus* (Figure 2) the two lobes are not synchronous in their action; "that of one side undergoes its recovery stroke at the precise time when the other is in the phase of effective beat" (THOMPSON & SLINN, 1969). In *C. cynara* there is synchronous action with the cerata, each side in balance with the other (Figure 15 B). Here all cerata are poised for the backward thrust, the posterior ones already in this process. Synchronous beating also occurs in *Akera* and *Gastropteron*.

It is not known why opisthobranchs swim in the various manners discussed. Some are weak swimmers and once in the water column are carried by the currents. *Coryphella cynara* is considered a strong swimmer and has efficient means of swimming.

Many opisthobranchs have no apparent direction to their swimming, such as the lateral body benders. On the other hand, animals using notal and parapodial methods of swimming have more control of the direction of their movement.

Swimming in many cases, as in that of *Nembrotha eliora*, is an escape response while in others it is apparently merely a means of moving from one place to another. This applies particularly to *Melibe leonina*, which is commonly found in kelp beds where it seems advantageous to be able to swim from one kelp frond to another, if the animal is dislodged.

SWIMMING PROSOBRANCHS

There are 8 species, representing 3 orders, of swimming prosobranchs.

Solariella nektonica, an archaeogastropod, is about 7 mm in greatest dimension; it has been recorded from 31°35′18″ N, 130°06′30″ E. When the animal swims, the foot expands to 2 - 3 times its usual dimensions and the shell is kept on the upper side. When movement is suspended and the animal is ready to descend (see Figure 16), the shell is downward.

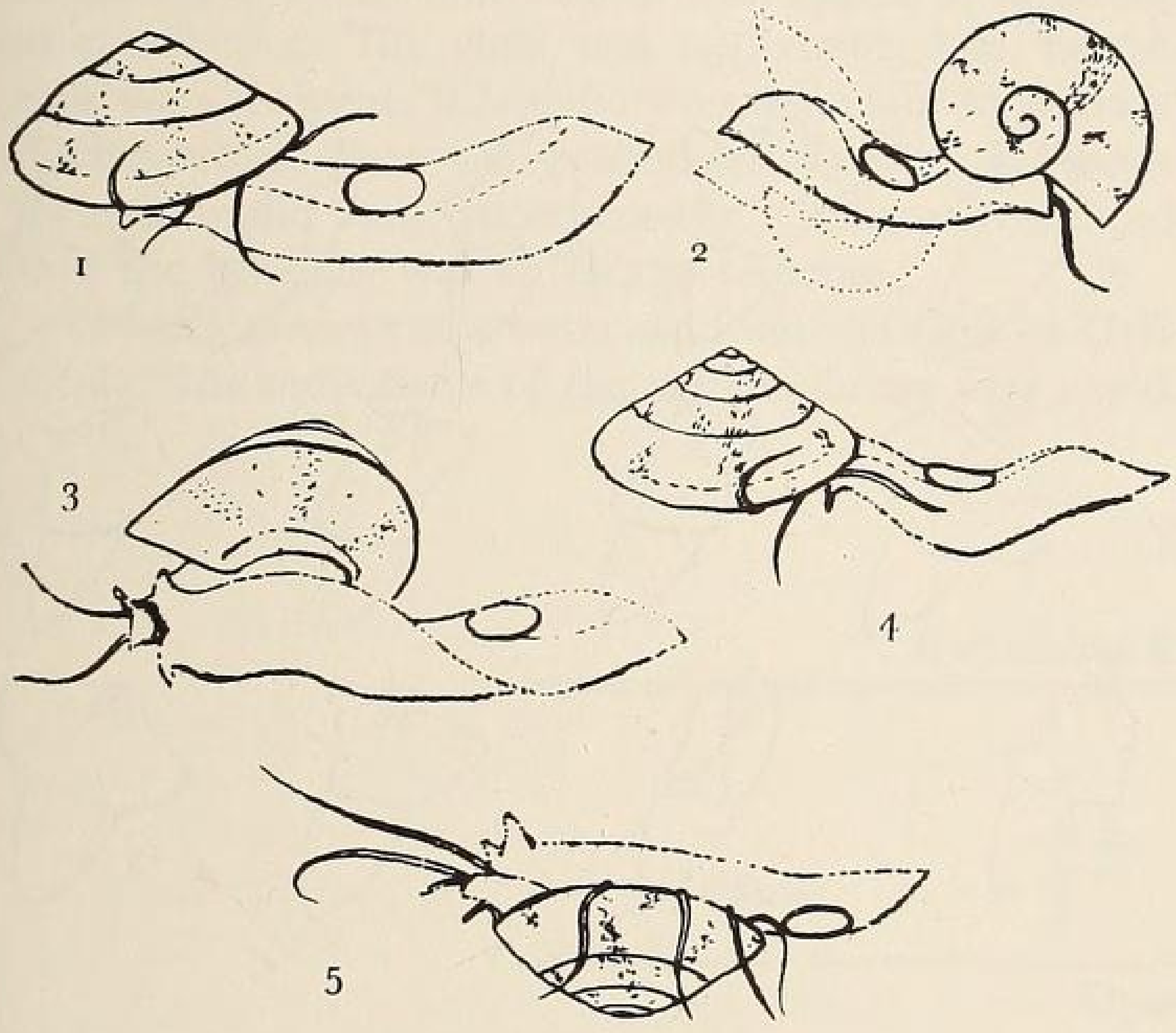


Figure 16

Movement of swimming in *Solariella nektonica.*

1 to 4: Movement of swimming – 5: animal descends when swimming is suspended, after OKUTANI, 1961

"The expanded posterior part of the foot is twisted at a right angle, thus it becomes like the tail of a tadpole in appearance and in function. This gastropod swims in a rather straight direction, controlling the swimming by itself. It is not considered to be a demented movement." (OKUTANI, 1961).

Ampullarius, according to PELSENEER (1935), swims by using quick movements of the snout and cephalic appendages. *Polinices josephinus* is reported by ZIEGELMEIER (1958) to swim by thrashing the extended propodium (see Figures 17, 18). ZIEGELMEIER's film was taken at 16 frames per second. At this speed one swimming motion or "stroke" takes 33 frames or 2 seconds. This species can swim with the shell dorsal or ventral to the foot.

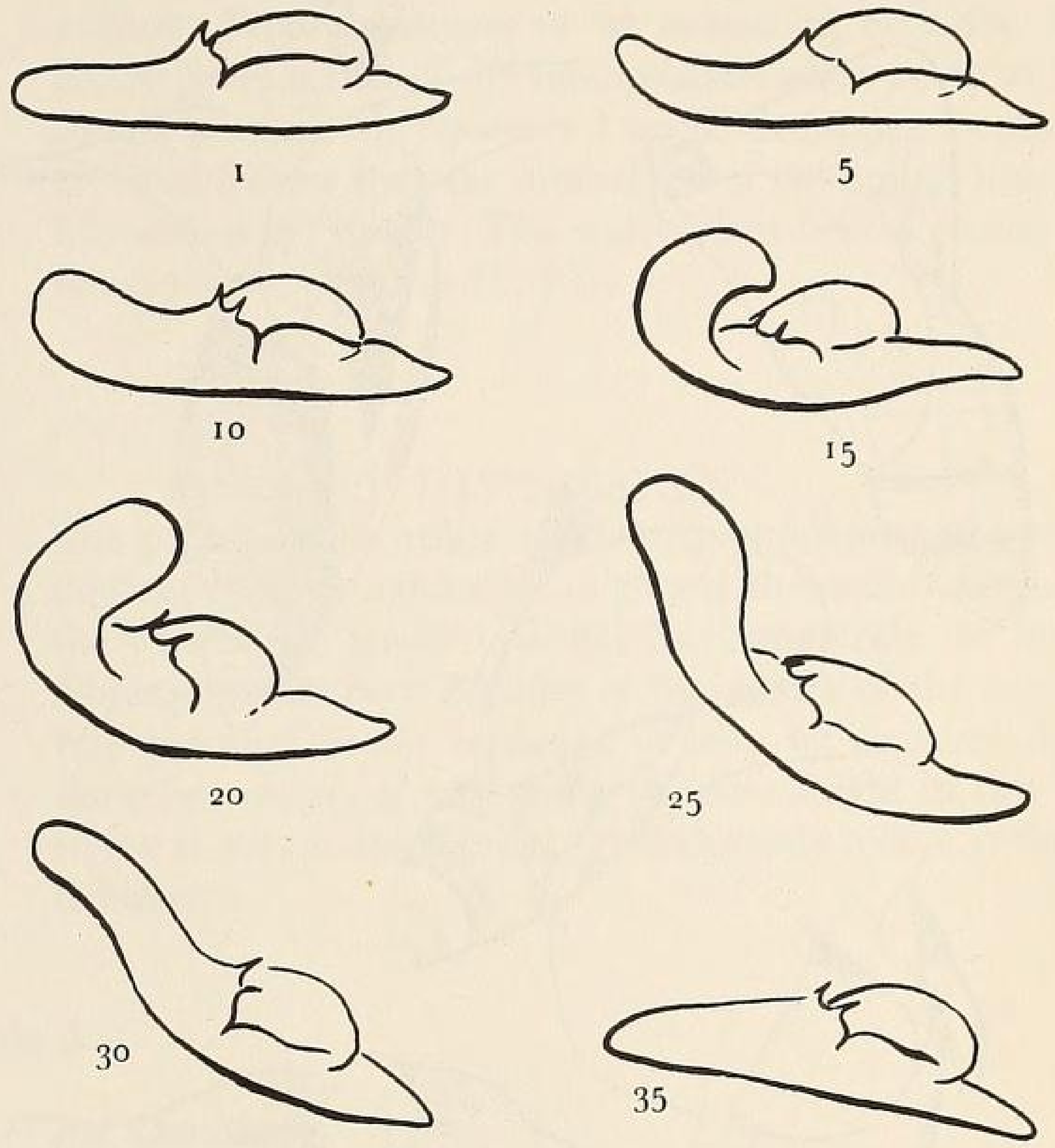


Figure 17

Polinices josephinus, a swimming prosobranch in normal position. Filmed at 16 frames per second; after ZIEGELMEIER, 1958

EDWARDS (1969) writes that *Olivella biplicata,* in an escape response to *Pisaster* will rear up on the hind portion of its foot, withdrawing the propodium and throwing the parapodia forward; frequently the snail will flip over backwards. The snail pumps the expanded metapodium violently up and down, lifting the animal off the substrate and carrying it away some 5 - 10 cm in a form of upside-

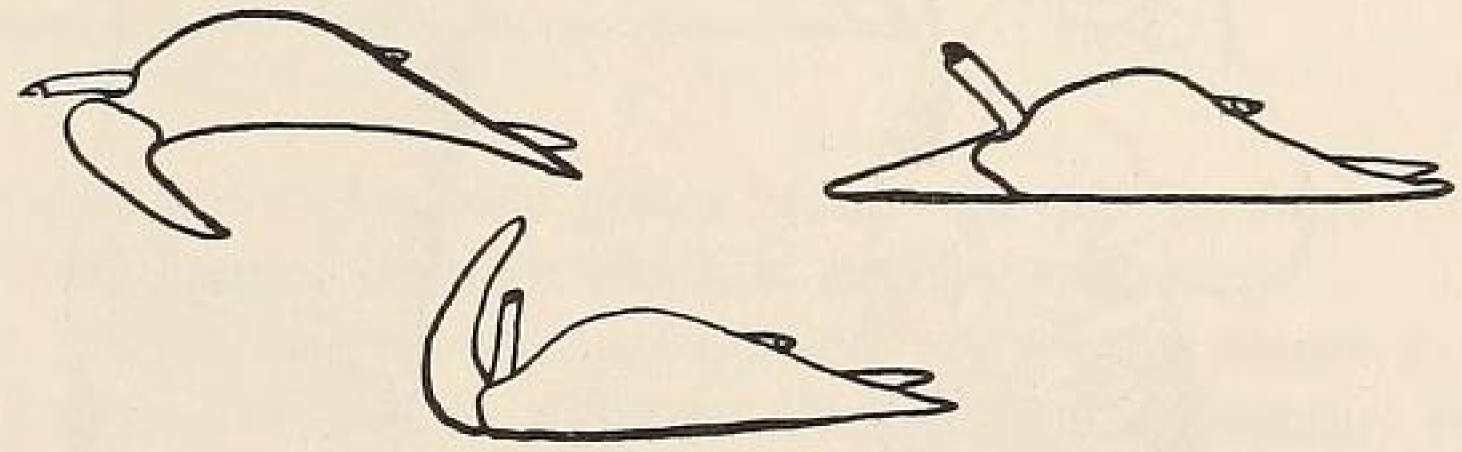


Figure 18

Ancillista cingulata utilizes the propodium in swimming, after WILSON, 1969

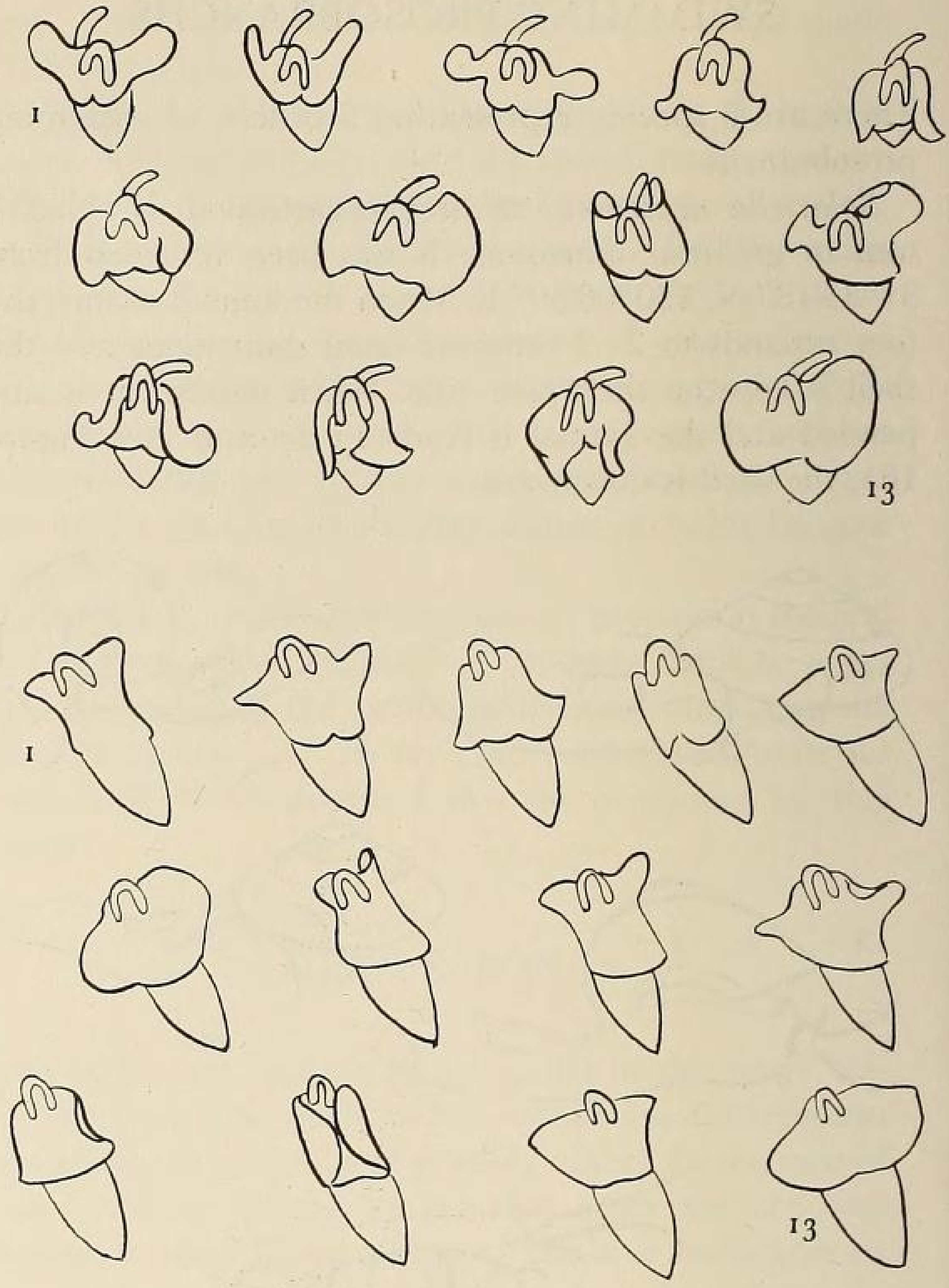
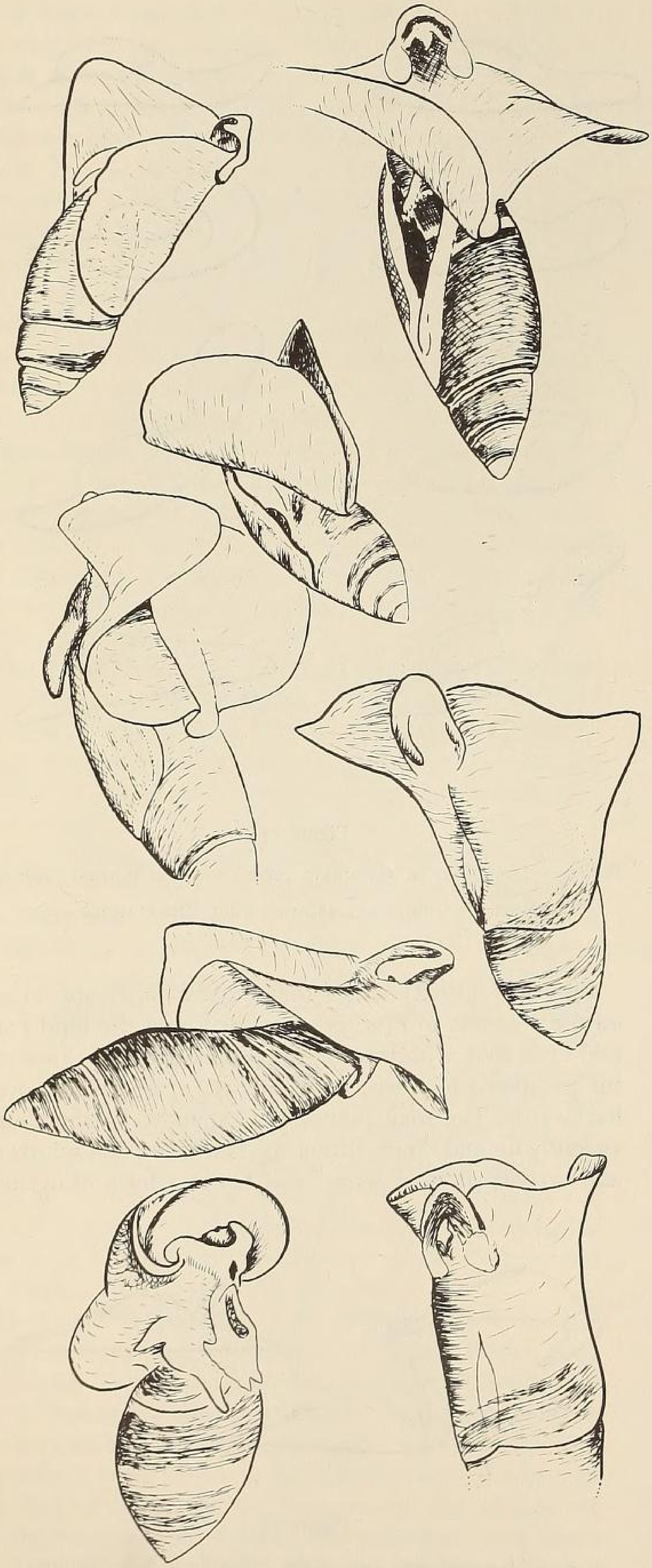


Figure 20

Olivella zanoeta; swimming rate is 240 strokes per minute. Two sequences are represented here

down swimming. This metapodial swimming response is qualitatively distinct from any previously reported escape behavior by a gastropod. It is effected by holding the parapodia close to the sides of the shell, especially at the anterior end, so the vigorous down beats of the large, horizontally extended metapodium force water down and back, lifting the gastropod up and propelling it forward.

WILSON (1969) reports on the swimming behavior of *Oliva tehuelchana, Olivella verreauxii* and *Ancillista cingulata*. The 2 former swim by the lateral wing-like flaps



(<— adjacent column)

Figure 19

Olivella zanoeta filmed with a single lens reflex camera with strobe light to stop the action of the metapodium. Bottom of tank, relative to animal, is down of the metapodium, the latter utilizes the propodium. The metapodium characteristically folds over and covers the shell in members of the Olividae.

The propodium is used as the primary swimming organ in *Ancillista cingulata* with the metapodium trailing. *Ancillista* swims in a jerky manner reminiscent of the random swimming movements of scallops (WILSON, 1969). "The propodium repeatedly flapped backwards from the horizontal plane, first dorsally and then ventrally at regular intervals of slightly more than one second. Each movement threw the animal forward a distance varying between 5 and 15 cm. The ventral beat appeared to be the most effective. The shell was uppermost, but 'barrel-rolls' were frequent. This activity continued for 45 seconds, during which time the propodium flapped 35 times. Swimming did occur spontaneously." WILSON concluded that the behavior was an escape response.

Olivella zanoeta is a swimmer from the Gulf of California. The movements of the metapodia are very rapid, causing the snail to move about in a somewhat irregular manner. Motion pictures of its swimming behavior did not stop the action of the metapodium when taken at 24 frames per second. However I could determine from individual frames that the animal has a swimming rate of 240 strokes per minute. This was evident from 6 frames of the sequence (Figures 19, 20).

DISCUSSION

The prosobranchs utilize the foot, propodium and metapodium type of undulation to propel themselves through the water. The family Olividae has apparently the most swimming members. Because of the nature of the escape response of *Olivella biplicata,* it may be assumed that the other species of swimming Olividae might in fact be trying to escape from predators commonly found in their habitats.

Table 3

Swimming Rates and Duration

Species	Swimming Type	Strokes per Minute	Duration
		Opisthobranchs	
Akera bullata	pf	120	up to ½ hour
Coryphella cynara	bs	44	
		46	over 45 minutes
Dendronotus giganteus	lb	45	—
Nembrotha eliora	lb	90	few seconds
Pleurobranchus tuberculatus	un	55 - 60	may be several hours
		Prosobranchs	
Ancillista cingulata	upro	46	45 seconds
Olivella zanoeta	mf	240	few seconds
Polinices josephinus	upro	30	—

CONCLUSION

Swimming gastropods use a variety of structures to effect swimming: the notum, parapodium, metapodium, propodium, and foot. The entire body can be used in a horizontal or vertical plane. Some species use a combination of 2 types of swimming: the entire body and the notum. Some use the cerata in a "breast stroke" rowing movement and one group utilizes the parapodia to form an opening through which to expel water.

If motion pictures are utilized to a greater extent, more variation in the different methods of swimming may become evident. Special care needs to be taken in acquiring additional data on rate, duration, and circumstances promoting swimming. Tables 1, 2, and 3 summarize much of what is known about swimming gastropods.

Several aplysids were not included, however, as the literature refers to swimming structures rather than to actual swimming.

Coryphella cynara possesses remarkable stamina in its swimming. However, as yet I do not know why this benthic nudibranch shows this behavior. The long swimming duration, I can theorize, may be related to the quest for food or to breeding behavior.

Nembrotha eliora shows a swimming behavior that is an escape reaction from its prime predator, *Roboastra* sp. Both are benthic species and apparently abundant in water 45 - 90 feet deep. *Roboastra* attains a length of up to one foot and more and is very swift in capturing the smaller *N. eliora* in its buccal envelope. *Nembrotha eliora* seems to sense the presence of *Roboastra* from several centimeters away and will avoid it by crawling away from it almost at a right angle.

The method of swimming of *Coryphella iodinea* is illustrated for the first time. Selected examples from the literature are used to illustrate the different types of swimming listed in Table 1.

ACKNOWLEDGMENTS

I would like to thank Dr. Dwight W. Taylor for his constructive remarks and introduction to the prosobranchs. Mrs. Carol Skoglund and Mr. H. Schroeder were very helpful; Mrs. Susan Kreml assisted by translating some French references. Dr. Alison Kay, Mr. Steven J. Long and Mr. James R. Lance offered additional data or specimens. Mr. Boris Innocenti provided a number of *Nembrotha eliora* and *Roboastra* sp. Hans Bertsch and Gladys Lytle critically read the manuscript. Much appreciation goes to my wife for her aid and support while this paper was being prepared.

ADDENDUM

It has been brought to my attention that perhaps more pelagic nudibranchs should be considered, including STEINBERG's (1956) report on *Cephalopyge trematoides* (CHUN, 1889). STEINBERG has observed it swimming but does not mention how it swims. Being a pelagic species, *C. trematoides* most probably is a floater with its movements augmented by some swimming effort.

Gordon Robilliard (pers. comm.) has observed 4 other species of swimming opisthobranchs. *Cumanotus beaumonti* uses its cerata, *Tritonia gilberti* swims by dorsal-ventral flexings, *Dendronotus dalli* by lateral bending of the body and *Coryphella longicaudata* by lateral bending, while also twisting in a screwshape from front to back.

Richard A. Roller (pers. comm.) observed *Tritonia gilberti* in an escape response from the sun-star, *Pycnopodium helianthoides.*

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