A New Species of Anaspidean Opisthobranch from the Gulf of California

(Mollusca : Gastropoda)

BY

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(1 Map; 15 Text figures)

INTRODUCTION

THE GULF OF CALIFORNIA abounds in its variety and number of species of opisthobranch gastropods. These include a fair mixture of Californian, Panamic, Indo-Pacific, and circumtropical species. The order Anaspidea is quite well represented in the fauna of the Gulf. Eight species of anaspideans have been reported from these waters. Of these, *Dolabrifera dolabrifera* (Rang, 1828), *Stylocheilus longicauda* (Quoy & Gaimard, 1824), *Aplysia parvula* Mörch, 1863, and *Aplysia juliana* Quoy & Gaimard, 1832, are of circumtropical distribution. KEEN (1971: 810) states that *Dolabella auricularia* (Lightfoot, 1786) is widely distributed in the Indo-Pacific. *Dolabella californica* Stearns, 1877 is known only from the Gulf. MARCUS & MARCUS (1970: 191) consider the *Dolabella californica* of MACFARLAND (1966) to be synonymous with *D. auricularia*. A formal synonymy of the 2 species is not given, however, and therefore 2 distinct species will be recognized here. The remaining 2 species, *Aplysia californica* Cooper, 1863 and *A. vaccaria* Winkler, 1955 are known from the coast of California as well as from the Gulf.

On December 23, 1970, some algal material (*Padina* sp.) was collected near San Carlos, Sonora, Mexico, to be used as a background for photographing several opisthobranchs collected the previous day. It was noted, however, that another opisthobranch was crawling actively along the algal surface. Direct observation of more of the same algae yielded several additional individuals of this dolabriferid anaspidean. Subsequent investigation of the material showed this animal to belong to an undescribed species, readily assignable to the genus *Phyllaplysia*.

Additional observations and specimens were obtained on a trip to Puertecitos, Baja California, in the spring of 1972. Two animals of the same species were collected on March 28, 1972 from the intertidal volcanic shores near Puertecitos.

Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.

Diagnosis: Penis armed; penial spines mammiform; penis tip cleft dorsally. Male aperture located antero-ventrally to right eye. Hermaphroditic gonopore located near anterior region of dorsal slit. Gonad narrow, elongate. Duct of bursa copulatrix arising from common atrium. Radular formula approximately 18 × 8-21 · 1 · 1 · 1 · 8-21. Rachidian teeth tricuspid, cusps acute; first pleural teeth tall, with 3 obtuse cusps; other lateral teeth short, with broad, flattened edge and 2 adjacent, smaller cusps; labial plates armed; labial armature tall, mammillate; jaws armed; masticatory armature of dense, tall, hook-tipped rodlets; gizzard teeth cornucopiate, uniform in structure. Shell a flat plate with central calcified portion and transparent margin; shell composed of concentric rings surrounding central apex. Cerebral commissure length approximately equal to cerebral ganglion diameter. Body color uniform olive green with scattered white spots; body often with minute papillae; papillae, when present, highly variable in shape and number. Body length not exceeding 45 mm; body slender, visceral hump reduced. Rhinophores short, bulbous, slit from distal ends ½ their length. Cephalic tentacles slit entire length to base; cephalic tentacles commonly held at right angles to each other in actively crawling animals. Oral tentacles elongate triangular, acute at tips. Foot broadest just posterior to middle of body in actively crawling animals; foot margin and edge of dorsum joined throughout.

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Type Material: The holotype of *Phyllaplysia padinae* is deposited in the Invertebrate Zoology Type Collection of the California Academy of Sciences, San Francisco, California, where it bears the number CASIZ 591; also deposited are the shell (CASIZ 592) and radula (CASIZ 593) of paratype specimens. Other paratype material remains in the private collections of the authors.

Name: The specific name *padinae* is derived from the name of the dictyotalean phaeophyte alga *Padina durvillaei* Bory de Saint Vincent, 1827 on which the animal is most often encountered.

Taxonomic Position in the subclass Opisthobranchia:

APLYSIIDAE

Dolabriferinae

Phyllaplysia P. Fischer, 1872

Phyllaplysia padinae

WORLD SPECIES LIST

The following is a list of species names presently in use in the genus *Phyllaplysia*.

1. *Phyllaplysia brongniartii* (Blainville, 1825)
2. *P. depressa* (Cantraine, 1835)
3. *P. engeli* Marcus, 1955
4. *P. inornata* Bergh, 1905
5. *P. lafonti* (P. Fischer, 1870)
6. *P. ornata* (Deshayes, 1853)
7. *P. padinae* Williams & Gosliner, 1973
8. *P. paulini* Mazzarelli, 1895
9. *P. plana* Eales, 1944
10. *P. taylori* Dall, 1900
11. *P. varicolor* (Bergh, 1905)
12. *P. viridis* (Bergh, 1905)

Type Locality: The type locality of *Phyllaplysia padinae* is the San Carlos Bay region directly northwest of Guaymas, Sonora, Mexico. Individuals were encountered only on the outer coast of the point forming the southern portion of San Carlos Bay (27°55′N lat.; 111°05′W long.).

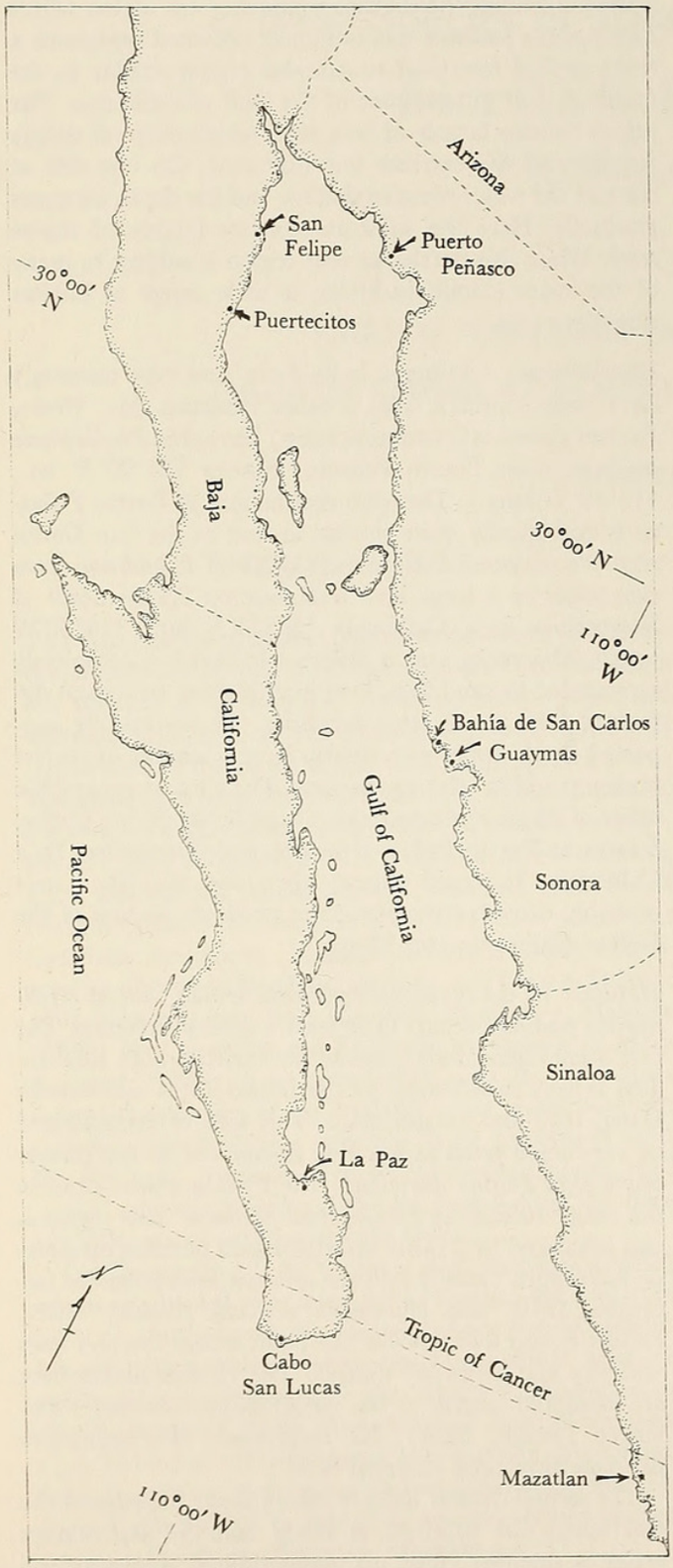
NATURAL HISTORY

Some of the qualitative aspects of the biodynamics of San Carlos Bay have been discussed by GOSLINER & WILLIAMS (1972: 425 and 432). Though San Carlos Bay represents a unique heterogeneous ecosystem, the reef region where *Phyllaplysia padinae* was originally collected represents a more typical intertidal to subtidal region similar to the major part of the coastline of the Gulf of California. The region consists largely of lava reefs which drop off deeply just beyond the extreme low tide zone. On one side of the reef the water remains shallow and the depth increases gradually. Here the substrate consists largely of coarse sand. While this particular reef region is subject to many of the same abiotic variables, a wide range of habitat diversity exists.

Distribution: Additional individuals (not type material) have been collected from 2 other localities. Mr. Wesley Farmer (personal communication) has taken *Phyllaplysia padinae* from Puerto Peñasco, Sonora (31°20′N lat.; 113°38′W long.). The open reef habitat at Puerto Peñasco is ecologically quite similar to that at the San Carlos reef. We collected 2 large individuals of *P. padinae* from tide pools on a large lava rock outcrop 2.4km north of Puertecitos, Baja California (30°25′N lat.; 114°40′W long.). This rocky area is different in that it is completely surrounded by sand flats. Despite this great ecological difference from the 2 other localities, the marine life supported by this volcanic outcrop is very similar in species make-up and in relative numbers. The present geographic range of *Phyllaplysia padinae* is from Bahía de San Carlos, Sonora to Puerto Peñasco, Sonora and Puertecitos, Baja California. It would appear, therefore, that the range probably extends throughout the northern portion of the Gulf of California (see Map).

Habitat: At the type locality (Bahía de San Carlos) *Phyllaplysia padinae* occurs in at least 2 distinct habitats. The first occurs immediately below the extreme high tidal region largely inhabitated by the isopod *Ligia occidentalis* Dana, 1853 and various crabs. This area is characterized by very small pools at low tide dominated by the phaeophyte alga *Padina durvillaei*. The *Padina* blades provide the major habitat of *Phyllaplysia padinae*. This region is also inhabited by 2 other opisthobranch herbivores, *Aplysia californica* (mostly juvenile animals as observed in December 1970) and *Haminoea vesicula* (Gould, 1855). *Padina* is also found below the point where the reef ends abruptly and drops off sharply. The *Padina* blades here are inhabited largely by the sacoglossan *Tridachiella diomedea* (Bergh, 1894). No individuals of *Phyllaplysia padinae* have been observed here.

The second distinct habitat occurs along the edge of the reef where the substrate is sandy and the supernatant water is shallow. Here, an undetermined species of the marine eel-grass *Zostera* grows rather sparsely relative to the vast beds of *Zostera marina* Linnaeus, on the coasts of



Map of the Sea of Cortez, Mexico

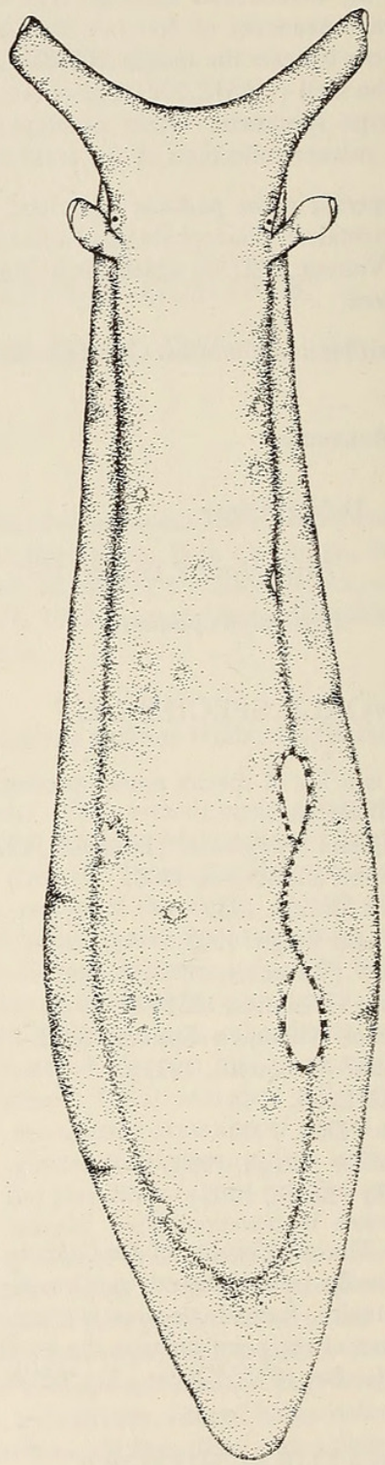


Figure 1

Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Dorsal aspect of a 12 mm long animal

Washington, Oregon, and California. Individuals of *Phyllaplysia* ***padinae*** were encountered crawling about the blades of the eel-grass in this more subtidal habitat.

The individuals of *Phyllaplysia* ***padinae*** from Puertecitos occurred only on *Padina durvillaei* in the mid-tide zones. Subtidally, the blades of *Padina* revealed no individuals of *P.* ***padinae*** (as was the case at the type locality) despite the fact that no individuals of *Tridachiella diomedea* were encountered either.

Locomotion: The locomotion of *Phyllaplysia* ***padinae*** is a distinguishing aspect of many smaller individuals (less than 20 mm in length). The initial movement of the animal firmly attached to the algal substrate involves the simultaneous arching of the central portion of the dorsum and the foot while the posterior-most portion of the body is moved forward. The animal then extends forward, returning the body to its dorso-ventrally flattened position. This process is repeated quite rapidly in a continuous cyclical process. This inch-worm-like form of movement was the only noticeable form of locomotion observed in the smaller animals. Actual rates of movement were not calculated, yet relative to other opisthobranchs it appears to be quite rapid and much more so than the common pedal wave action of other animals (see Figure 2).

Larger individuals of *Phyllaplysia* ***padinae*** (generally over 30 mm in length) move in the more conventional method for members of the genus. The anterior portion of the body moves forward first while the posterior half of the body remains stationary until after the elongation of the body and the anterior extension has been completed. Then the posterior section moves forward restoring the animal to its normal resting position as opposed to the full extension that occurs as an intermediate step in this process. At no point does any portion of the foot leave the substrate on which the animal is crawling as is the case with the smaller individuals.

Feeding: Feeding was observed in an aquarium. An individual of *Phyllaplysia* ***padinae*** collected at Puertecitos grazed upon the surface of *Padina durvillaei.* Grazing is accomplished by the movement of the animal over the algal surface, and the probing of the food substrate by the constant movement of the oral tentacles. The radula is periodically extended to scrape the surface of the algae, thereby ingesting epiphytic diatoms and the epidermal cells of the algae.

Examination of fecal matter from a 37 mm long animal kept in the aquarium revealed undigested surface cells of *Padina* together with the siliceous fragments of diatom tests.

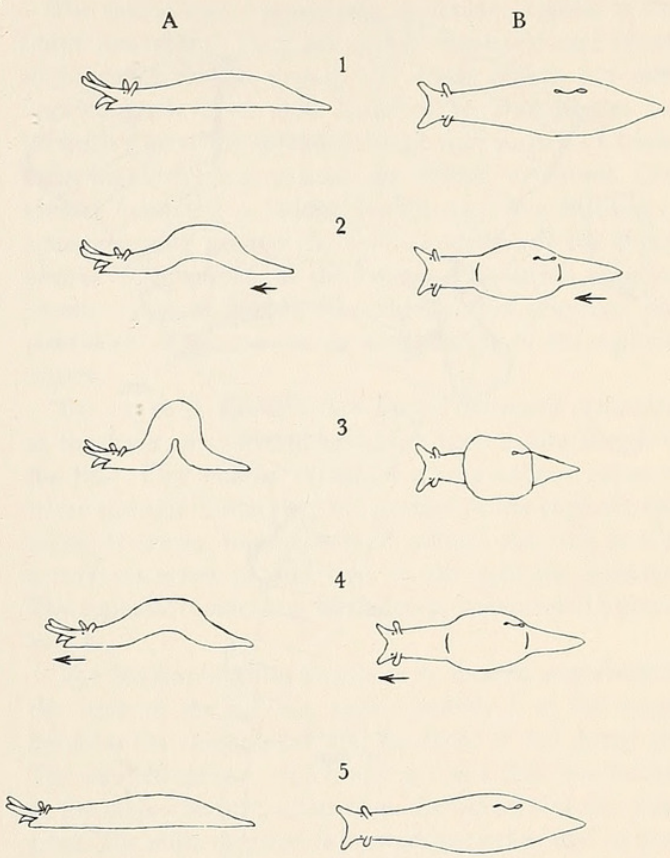


Figure 2

"Inch-worm" mode of locomotion in *Phyllaplysia* ***padinae*** drawn in linear sequence 1 through 5. A: left lateral view; B: dorsal view; 1: animal in normal position with foot attached to substrate throughout; 2: posterior end of body moves forward (arrow); 3: animal becomes momentarily stationary as dorsal arch reaches maximum height; 4: anterior region of body extends forward, reducing arch (arrow); 5: body returns to normal position as in 1, and process is repeated

Egg Mass: The egg mass of *Phyllaplysia* ***padinae*** is a flat ribbon found upon the blades of *Padina durvillaei* (see Figure 3). An egg mass collected at Puertecitos measured 7 mm in width, 12 mm in length, and 3 mm in height. Another egg mass found on the inside of a plastic container in which 2 animals were isolated for several days measured 5 mm in width, 18 mm in length, and 2 mm in height. The egg masses are rectangular in shape and of a brownish-green color, quite similar to the color of *Padina.* Three additional egg masses were found at Puertecitos on blades of *Padina,* their maximum length approaching 15 mm.

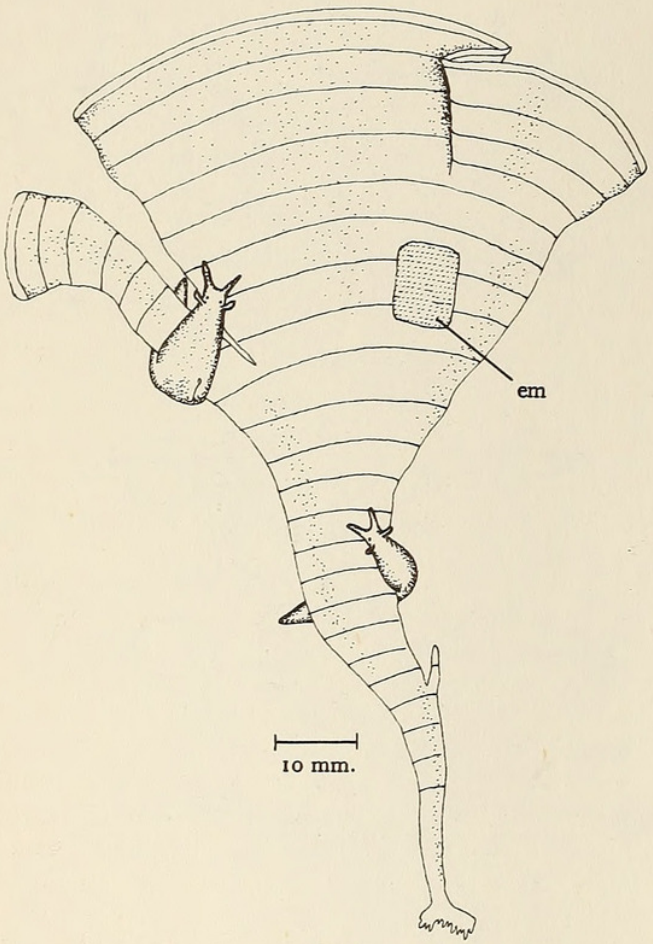


Figure 3

A blade of *Padina durvillaei* with two individuals of *Phyllaplysia padinae* and their characteristic egg mass
em – egg mass

MORPHOLOGY AND ANATOMY

External Characteristics: The ground color of *Phyllaplysia* ***padinae*** is olive green to brownish-green with random white spotting of the dorsal surface. The brownish-green ground color is very similar to the color of the host alga *Padina durvillaei*. The foot is brownish-green also, the large digestive gland being readily distinguished through the translucent ventral portion of the body. Several individuals exhibited scattered brown mottling on the dorsal surface; however, the plain green ground color without mottling is most common. The dorsal surface of some animals showed several white star-shaped markings. These markings are small papillae which may be totally absent in some individuals. One animal revealed 8 such papillae near the central portion of the body. The position and number of papillae are purely random, varying considerably in different individuals. The papillae are very variable in shape (Figure 5). The majority are wider than long, and composed of a cluster of small projections from a common base. Less common are papillae of only

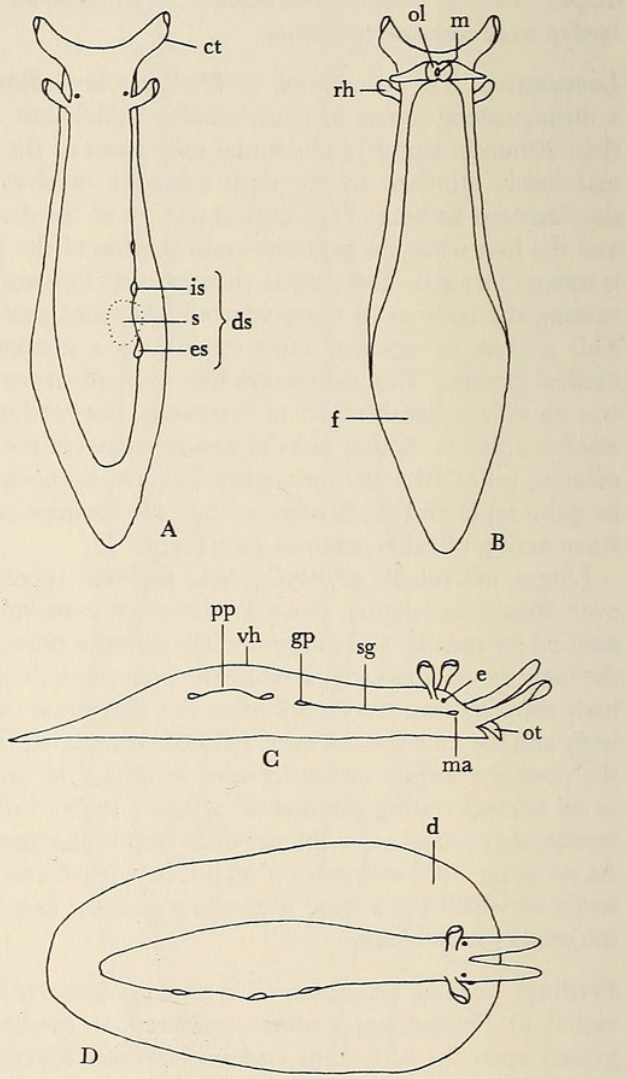


Figure 4

Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Diagram of external features: A - dorsal view; B - ventral view; C - right lateral view; D - dorsal view of contracted animal
ct – cephalic tentacle d – dorsum ds – dorsal slit (gill slit)
e – eye es – excurrent (anal) siphon f – foot
gp – gonopore (common genital duct) is – incurrent siphon
m – mouth ma – male aperture (male gonopore)
ol – oral lip (outer lip) ot – oral tentacle pp – parapodium
rh – rhinophore s – shell sg – seminal groove
vh – visceral hump

one tapering individual protuberance, which may be longer than wide. These papillae taper at the ends and do not exceed 0.5 mm in length.

The body shape is typical of the subfamily Dolabriferinae. The foot is broad throughout, though it may vary in shape considerably when the animal is contracted or extended. The body of the animal may exhibit 2 characteristic positions. When the animal is not moving, the body is contracted with the front of the foot protruding in front of the head, with only the cephalic tentacles exceeding the broad anterior region of the foot (Figure 4D). When in this position, the cephalic tentacles are folded together and point straight forward, forming an angle of 180° with the antero-posterior median line of the body. A significant change in shape and size of the body can take place in this non-motile position. A 22 mm long extended animal measured only 18 mm when contracted. Another animal measured 32 mm extended, 26 mm contracted. The largest animal observed measured 45 mm when extended,

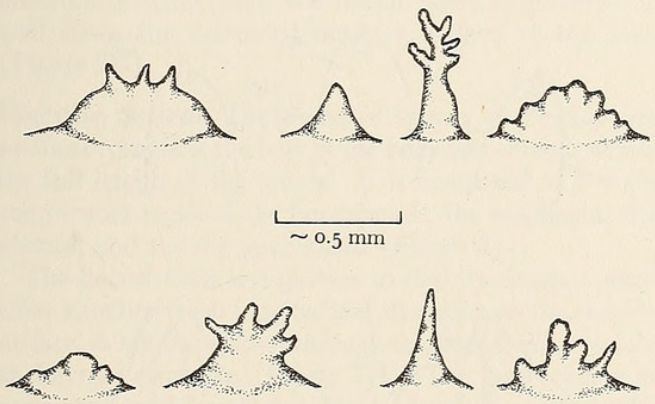


Figure 5

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Variation in dorsal surface papillae

35 mm when fully contracted. When contracted, the body is more elliptic, less elongate. When the animal is moving or in the extended position, the body becomes considerably elongated and narrow, the anterior margin of the foot extends behind the head and the cephalic tentacles spread apart, forming a near right angle between the individual tentacles. When the body is in motion, the foot is widest posterior to the middle of the body (Figures 1 and 4B). When contracted, the foot is widest in the head region, or just anterior to the middle of the body. The living animal is most commonly seen in the extended position and only rarely is the contracted position assumed.

The rhinophores are partially auriculate, typical of the order Anaspidea. They are rather shortened and blunt, slightly club-shaped toward the distal region and cleft approximately ½ of their length. The rhinophores are greenish with white speckling which may form 2 - 4 transverse bands or rings around the central structures. One animal exhibited a reddish-brown speckling forming a transverse ring around the central portion of the rhinophores. Rhinophores in the holotype measured approximately 1 mm in length. The rhinophores originate just posteriorly of the eyes on the dorsal edges of the cephalic region.

The cephalic tentacles are large, thickened structures at the front of the head and cleft their entire length to the base. One animal exhibited a very narrow stripe of white pigment lining the cleft portion of the cephalic tentacles. However, the majority of animals observed showed a uniform green ground color in the cephalic tentacles. The cephalic tentacles in the holotype measured 2.5 mm in length.

The hermaphroditic gonopore is located anteriorly to the front of the gill slit, approximately ¾ of the length between the rhinophores and the front of the dorsal slit. The seminal groove, which appears as a thin line leading to the male aperture, arises from the anterior of the gonopore. The male aperture is located just below and in front of the right eye (Figure 4C). The small parapodia form a cavity (the gill slit or dorsal slit) containing the gill and other organs, located slightly to the right of the middle of the body. The incurrent opening lies directly in front of the excurrent opening. The posterior end of the excurrent siphon is located toward the tail of the body, on the posterior slope of the visceral hump. The parapodia are greatly reduced as in other members of the Dolabriferinae. The right parapodium overlaps the left parapodium and covers the middle of the dorsal slit. In the living holotype of *Phyllaplysia padinae* the right parapodium is slightly speckled on its edge with alternating dark and light pigment.

Radula: Inside the buccal mass is contained the tubular horseshoe-shaped radula supported by the basal musculature of the odontophore. The radula is golden brown in color and easily distinguishable when the buccal mass is opened dorsally. The radula is composed of approximately 18 rows of trimorphic teeth. The rachidian column is composed of relatively short teeth, narrow and tricuspid above, broader and bilobed behind. The middle cusp is elongate and pointed at the tip. The 2 adjacent cusps are shorter and rounded, and are equal in shape and size (Figure 6).

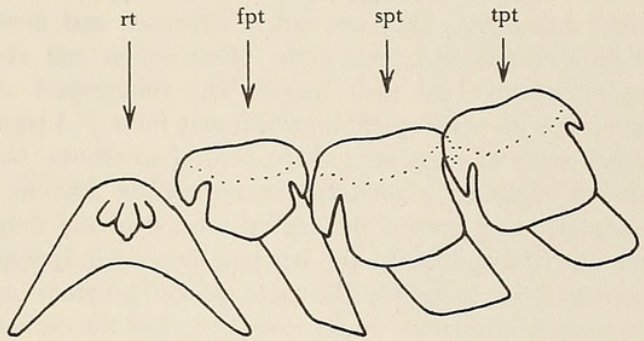
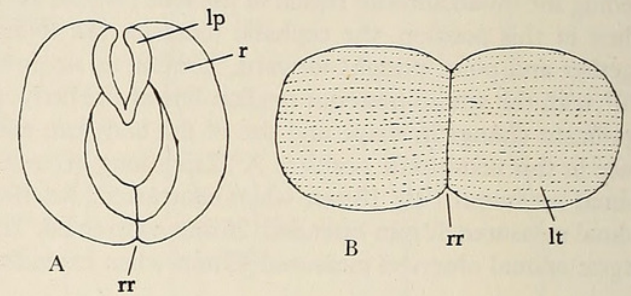


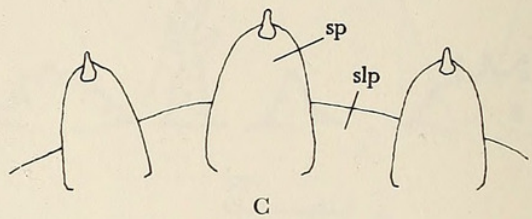
Figure 6

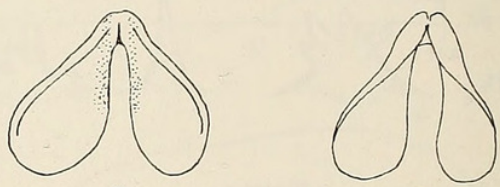
Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Radula: elements of 8th half row from right side
fpt – first pleural tooth fopt – fourth pleural tooth
rt – rachidian tooth spt – second pleural tooth
tpt – third pleural tooth

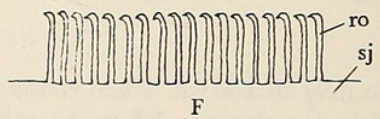
The first lateral column is composed of taller, tricuspid teeth. These teeth are the tallest in the radula and extend slightly above the rachidian and the other lateral teeth. The 3 cusps of the first lateral teeth are blunt and somewhat rounded. The median cusp is slightly angled in the middle, giving rise to 2 relatively straight edges. The 2 adjacent cusps are subequal and rounded at the tips. There exists only 1 column of these teeth on each side of the rachidian column, making 2 such columns in all. The remaining lateral teeth are very wide but shorter than the first laterals. These teeth make up the dominant form in the radula and are relatively uniform in shape and size from the inner to the outer columns. They are also tricuspid with 1 quite reduced, somewhat acute lateral cusp. The inner lateral cusp is larger and varies in shape from a blunt, rounded tip to a relatively tapered, subacute one. The central cusp is very broad with a uniform smooth edge and slight curvature. The bases of these teeth

(adjacent column →)









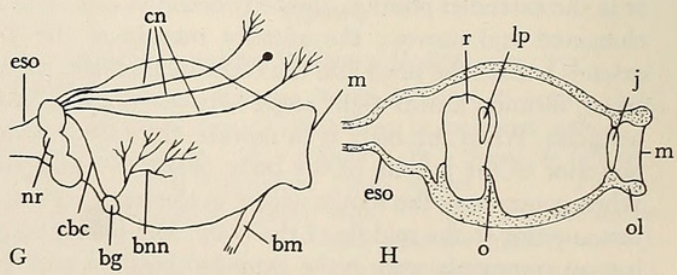


Figure 7

Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Elements of the buccal mass
A: anterior view of radula and labial plate; B: the radula as seen flattened on a microscope slide; C: elements of the labial armature (anterior surface of the labial plate); D: jaws, anterior surface (stippling represents area covered with armature); E: jaws, posterior surface; F: elements of the jaw armature; G: right lateral view of buccal mass; H: sagittal section of buccal mass (the anterior is to the right)
bg – buccal ganglia bm – buccal musculature
bnn – buccal nerve network cbc – cerebro-buccal connective
cn – cephalic nerves eso – esophagus j – jaws
lp – labial plate lt – rows of lateral teeth m – mouth
nr – nerve ring (central nervous system) o – odontophore
ol – oral (outer) lip r – radula ro – rodlet
rr – rachidian row sj – surface of jaw
slp – surface of labial plate sp – spine

are quite broad in comparison to the slender elongate basal structure of the first lateral teeth. The lateral teeth may vary in number from 8 to 21 per row. The overall radular formula is therefore 18 × 8 - 21 · 1 · 1 · 1 · 8 - 21.

Jaws and Labial Armature: The muscular labial plate forms a V-shaped structure in the dorsal open area of the horseshoe-shaped radula (Figure 7A). This structure is embedded with several tall, mammiform spines with acute apices. These elements comprise the labial armature and line the anterior face of the labial plate.

The jaws are composed of 2 somewhat flattened spoon-shaped plates attached dorsally at their narrow ends. The jaws form an inverted V-shaped structure. The rounded distal ends fold inward creating a tapered funnel-shaped structure as viewed dorsally. The jaws are located within the buccal mass, anteriorly to the radula and just posteriorly to the outer (oral) lip. In addition to the labial armature, the jaws are also densely armed with many tall, narrow rodlets with hooked tips. The area covered with armature extends from the dorsal point of juncture to well down the expanded anterior surface of the jaws (Figure 7D).

Digestive System: The digestive system of *Phyllaplysia* ***padinae*** comprises the bulk of the body and extends nearly the full length of the animal. It is composed of 4 main conspicuous regions: the buccal mass, the esophagus, the gizzard, and the digestive gland (Figure 8).

The buccal mass is a globose to slightly elongate muscular structure with longitudinal striations on the outside surface. A sagittal section through the buccal mass reveals its internal structure (Figure 7H). The large radula is positioned on the muscular, basal odontophore. From the opening formed by the curvature of the radula extends the armed labial plate through which begins the esophagus. Just anterior to the radula and labial plate is a thin membranaceous tissue upon which are located the jaws. Anterior to the jaws are the muscular, convoluted outer lip and mouth.

The esophagus forms no definite, easily distinguishable pharyngo-esophageal juncture with the buccal mass. Rather, the esophagus is formed by the gradual tapering off of the buccal area which narrows behind to join with the gizzard. The length of the esophagus does not exceed the length of the buccal mass nor that of the gizzard.

The pharyngeal or salivary glands are relatively wide but elongate organs which join the buccal mass by narrow ducts at the very posterior end of the buccal mass near the beginning of the esophagus.

The gizzard is also a rather globose to somewhat elongate structure, similar in shape to the buccal mass. The gizzard, however, is easily distinguished by a wide band

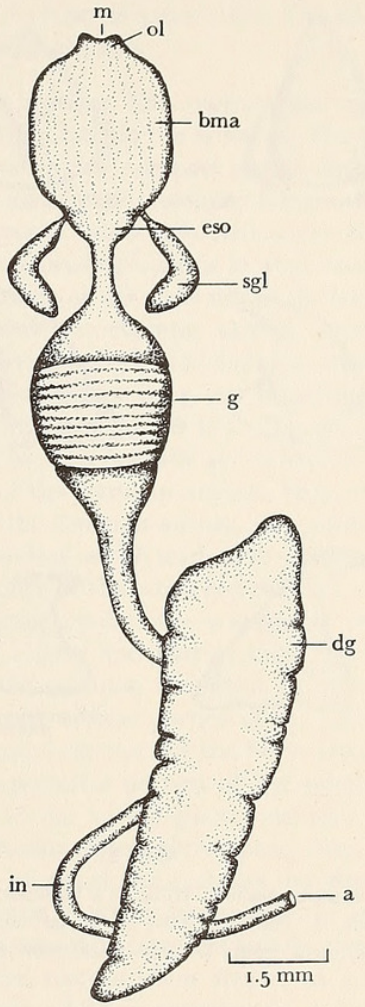


Figure 8

Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Dorsal view of digestive system
a – anus bma – buccal mass dg – digestive gland
eso – esophagus g – gizzard in – intestine m – mouth
ol – oral (outer) lip sgl – salivary (pharyngeal) gland

of transversely striated region which encircles the entire median portion of the gizzard (Figure 8). The posterior end of the gizzard tapers rapidly to form a narrow tube which enters the digestive gland. The stomach is that portion of the alimentary tract which is surrounded by the digestive gland. The intestine is then the portion of the tract which exits the stomach and digestive gland to the anus. The anus is located at the posterior opening of the dorsal gill slit (excurrent siphon).

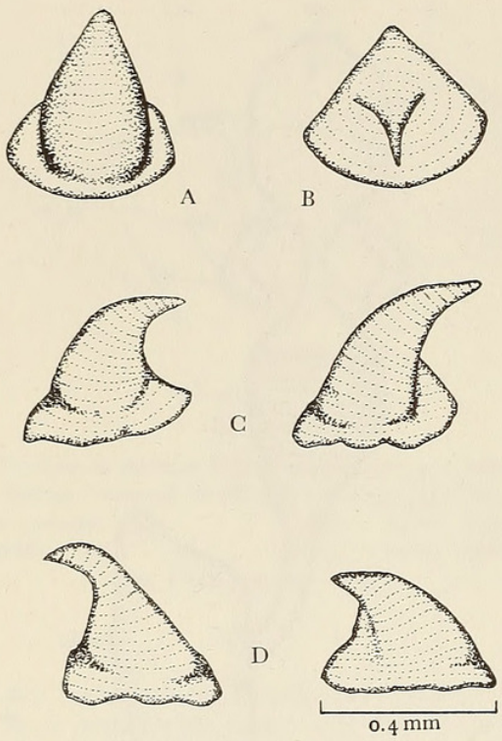


Figure 9

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Gizzard teeth. A: Posterior view; B: dorsal view; C: right lateral view of 2 different teeth; D: left lateral view of 2 different teeth

The digestive gland (liver) is the largest organ in the animal and is associated with the widest portion of the body just posterior to the middle. The digestive gland is deep brownish in color and has a fine granulated texture to its surface. This structure surrounds the stomach and is narrow and tapered at its posterior end. The anterior end is wider, rounded at the corners, and is somewhat concave to fit snugly over the posterior region of the gizzard. The posterior tip of the digestive gland projects into the very posterior portion of the visceral region.

The intestine which comes off from the middle of the digestive gland curves 180° to form a U-shape and exits at the posterior aperture of the dorsal slit (Figure 4A).

Gizzard Teeth: The gizzard of *Phyllaplysia padinae* contains many small gizzard teeth in the inside lining. These structures are cornucopiate in shape (horn-shaped) with a wide, flattened base and pointed apex (Figure 9). Three gizzard teeth from the holotype revealed approximately 15 transverse striations on the curved frontal surface of each. The gizzard teeth are uniform in shape and size, the only exception being that some are more severely hooked at the tips than are others. All gizzard teeth examined measured approximately 0.4 mm in diameter at the base and 0.5 - 0.6 mm in height. In all cases, the height to width ratio was greater than 1.

Shell: The shell of the holotype measured approximately 2 mm in length. A shell removed from a paratype measured about 2.5 mm in length. The shell is strongly built, thickened toward the center. The apex is in the center of the shell, surrounded by numerous concentric rings. The interior of the shell of the holotype is brown and lightly ridged with concentric rings which give rise to the trans-

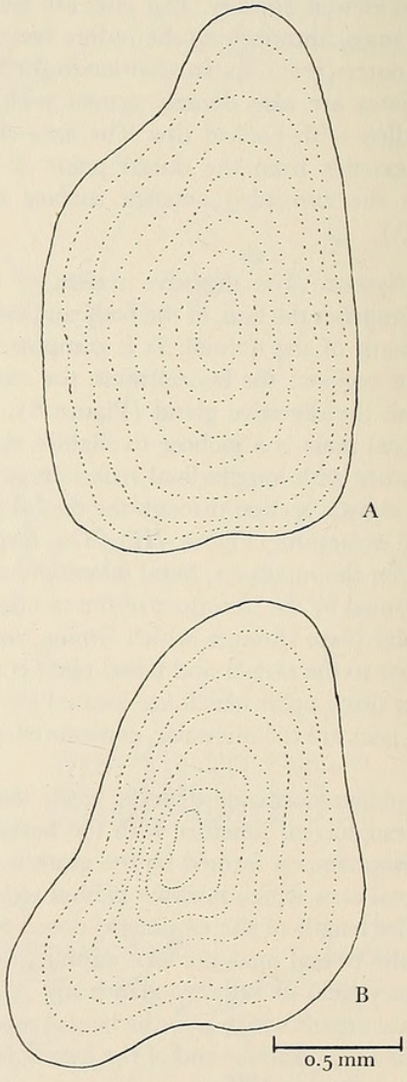


Figure 10

Phyllaplysia padinae Williams & Gosliner, spec. nov.
A: dorsal view of shell of holotype B: dorsal view of paratype shell

lucent, relatively thin outer margin of the shell. The shell, when examined in lateral view, is basically flattened with its highest point in the middle. The shape of the shell is triangular-roundish in outline with 3 usually distinguishable rounded corners. This gives the shell a somewhat elongate appearance (Figure 10).

The shell is contained inside the dorsal slit and is located on the dorsal surface of the mantle shelf.

Respiratory Apparatus: The respiratory organ is a pinnate structure representing a true ctenidium within the dorsal gill slit below the mantle shelf. The ctenidium of the holotype is 1.7 mm in length and is composed of a central mainstem which has a slight clockwise curvature when viewed dorsally. The mainstem has 8 - 9 side branches on each side. Each side branch is surrounded by a thickened U-shaped structure with a small cleft at its distal end (Figure 11). These strucures become progressively larger from the tip to the proximal origin of the ctenidium, giving the gill its tapered appearance. The gill is yellowish in color in living animals.

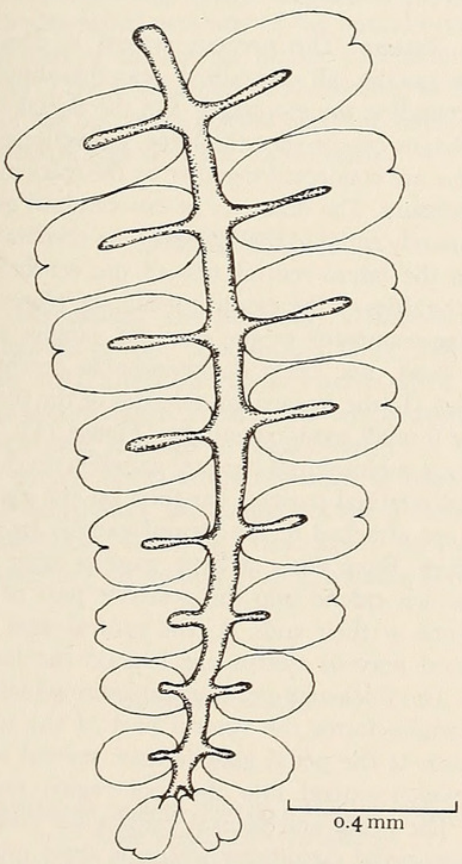
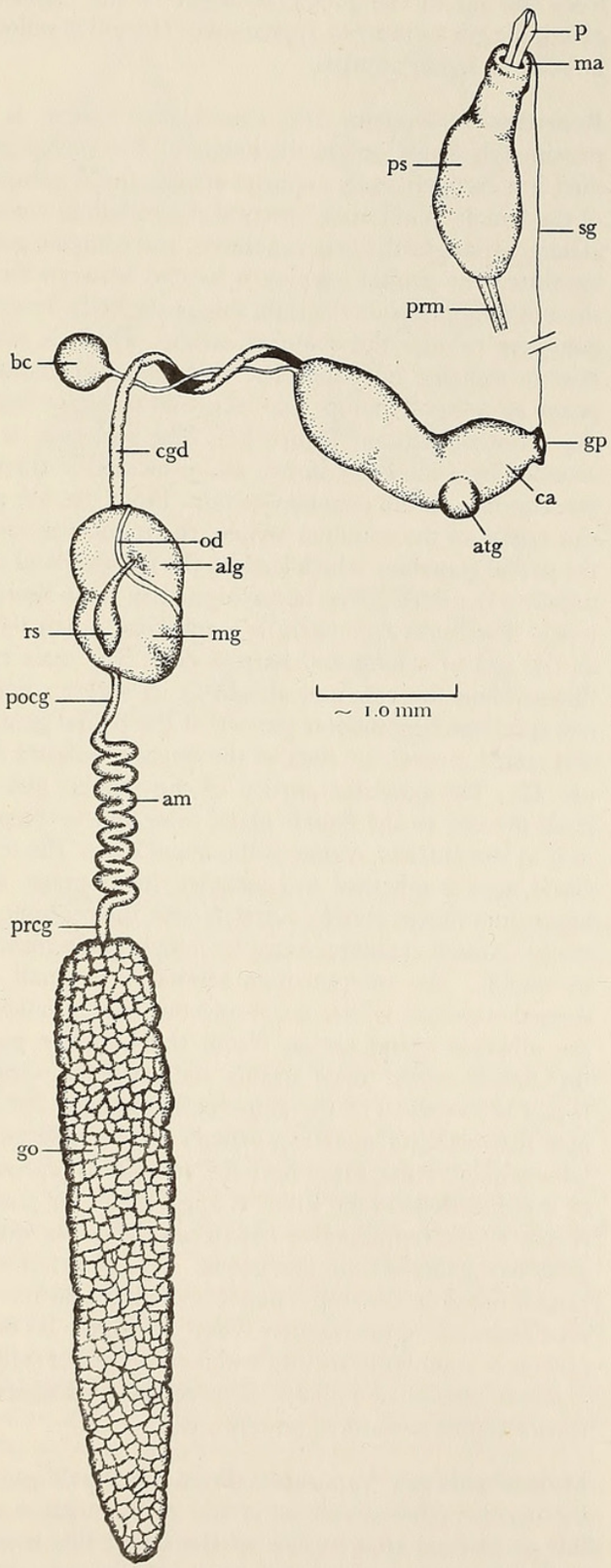


Figure 11
Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Dorsal view of ctenidium

Reproductive System: The reproductive system is approximately 6 mm long in the holotype. The pallial gonoduct is a comparatively compact system and is composed of the female gland mass, receptaculum seminis, common atrium, atrial gland, bursa copulatrix, and common genital aperture. The genital opening is located between the gill slit and rhinophore on the right side of the body. From the gonopore extends the common atrium, which is subglobose to elongate in shape. The bulbous atrial gland appears as a small bump near the mid-posterior end of the common atrium (Figure 12). The gonopore is surrounded by a muscular sheath and is located to the right anterior end of the common atrium. From the left anterior region of the common atrium, the tubular portion of the pallial gonoduct, which leads to the female gland mass, parallels the duct of the bursa copulatrix for a short distance. The bursa copulatrix is a spherical organ located at the end of a long and narrow duct. The duct enters directly into the common atrium at its anterior end. In one specimen, the tubular portion of the pallial gonoduct was coiled around the duct of the bursa copulatrix (Figure 12). The posterior portion of the tubular gonoduct leads directly to the female gland mass and is connected to it at the anterior region of the gland mass. The female gland mass is spherical and includes the albumen, membrane, and mucus glands, together with the receptaculum seminis, which emanates from the female gland mass near its middle. The receptaculum seminis is a small club-shaped structure which is conspicuous on the outside of the albumen gland region. From the posterior part of the female gland mass begins the coelomic gonoduct which is composed of the ampulla and gonad. The post-ampullar coelomic gonoduct bridges the ampulla and the female gland mass. From here the ampulla is represented by a tightly coiled tube which is apparent in the posterior region of the reproductive system and leads via the pre-ampullar gonoduct to the gonad. The ovotestis is the largest organ in the reproductive system and in the holotype measures approximately 3 mm in length. Its outside surface is granular in texture and is composed of well over a dozen individual follicles. The gonad is elongate and tapers slightly toward its posterior end.

Male Copulatory Apparatus: From the female gonopore the narrow, ciliated seminal groove can be seen as a thin line on the external surface of the body; this is on the right side of the animal and comprises the only connection between the main reproductive system and male



copulatory apparatus. The male gonopore is located just ventrally from the eye and to the right of the rhinophore (Figure 4C). The male copulatory apparatus is composed superficially of a highly muscular and striated penial sheath and shortened penial retractor muscle (Figure 13A). The penial sheath is sacklike in shape with a long tapering neck which exits from the body at the male aperture. The uncontracted sheath in the holotype measured about 3 mm in length. Inside the penial sheath is contained the contractile penis. The penis is characteristically cleft on its dorsal side from the distal tip to less than ½ its length. The penis, contracted in the holotype, measured 0.4 mm in width at the tip and 1.2 mm in length. On both sides of the cleft are embedded up to 5 penial spines which are arranged in 2 relatively uniform rows (Figure 13D). These spines are somewhat variable, but always mammiform and measure approximately 0.1 mm in diameter at the base. Their height may vary from 0.1 to 0.3 mm. The spines are broad at the base and taper to form acute and elongate tips (Figures 13F to 13I) .

Nervous System: The nervous system is composed of 10 major ganglia, all centralized near the anterior nerve ring surrounding the esophagus. On the dorsal surface of the esophagus can be seen the large, paired cerebral ganglia. These are connected together by the thickened cerebral commissure. The diameter of one cerebral ganglion is approximately equal to the length of the cerebral commissure. On the latero-ventral side of the cerebral ganglia and on the sides of the esophagus are the pleural ganglia which are connected to the cerebral ganglia by an extremely short, not easily distinguishable cerebro-pleural connective. To the inward lateral sides of the pleural ganglia arise 2 small rounded ganglia (Figure 14). These are the visceral-subintestinal-parietal ganglion on the left and the supraintestinal-parietal ganglion on the right. These ganglia are attached to the pleural ganglia by respective connectives. From each of these ganglia arise elongated nerves which extend into the posterior part of the body and branch at their ends. At the ventral-most region of the central nervous system are located the large pedal ganglia. The thickened pedal commissure which connects the 2 ganglia forms the ventral part of the nerve ring. From each of the pedal ganglia arise several long pedal nerves which extend into the foot region and ventral viscera. The pedal and pleural ganglia are connected by the pleuro-pedal connective which is short and difficult to distinguish. The cerebro-pedal connectives are very difficult to distinguish since the position of the pleurals bridges the 2 ganglia and makes observation of the direct connective between the cerebrals and pedals obscure. From the antero-dorsal region of the cerebral ganglia

(← on facing page)

Figure 12

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Dorsal view of reproductive system (not drawn to scale)
alg – albumen gland am – ampulla atg – atrial gland
bc – bursa copulatrix ca – common atrium
cgd – common genital duct go – gonad (ovotestis)
gp – gonopore (common genital duct) ma – male aperture
mg – mucus gland od – oviduct p – penis
prm – penial retractor muscle ps – penial sheath
psp – penial spine sg – seminal groove

arise the cerebro-buccal connectives which form the link between the cerebral and buccal ganglia. Also from this region arise several cephalic nerve networks which include the tentacular, rhinophoral, and optic nerves. These nerves may branch at their ends and extend into the anterior cephalic region of the animal. From the buccal ganglia extend the branched networks of the buccal nerves which surround part of the lateral surface of the buccal mass (Figure 14). The buccal ganglia are located at the ventral portion of the bucco-esophageal juncture, adjacent to the postero-ventral region of the buccal mass.

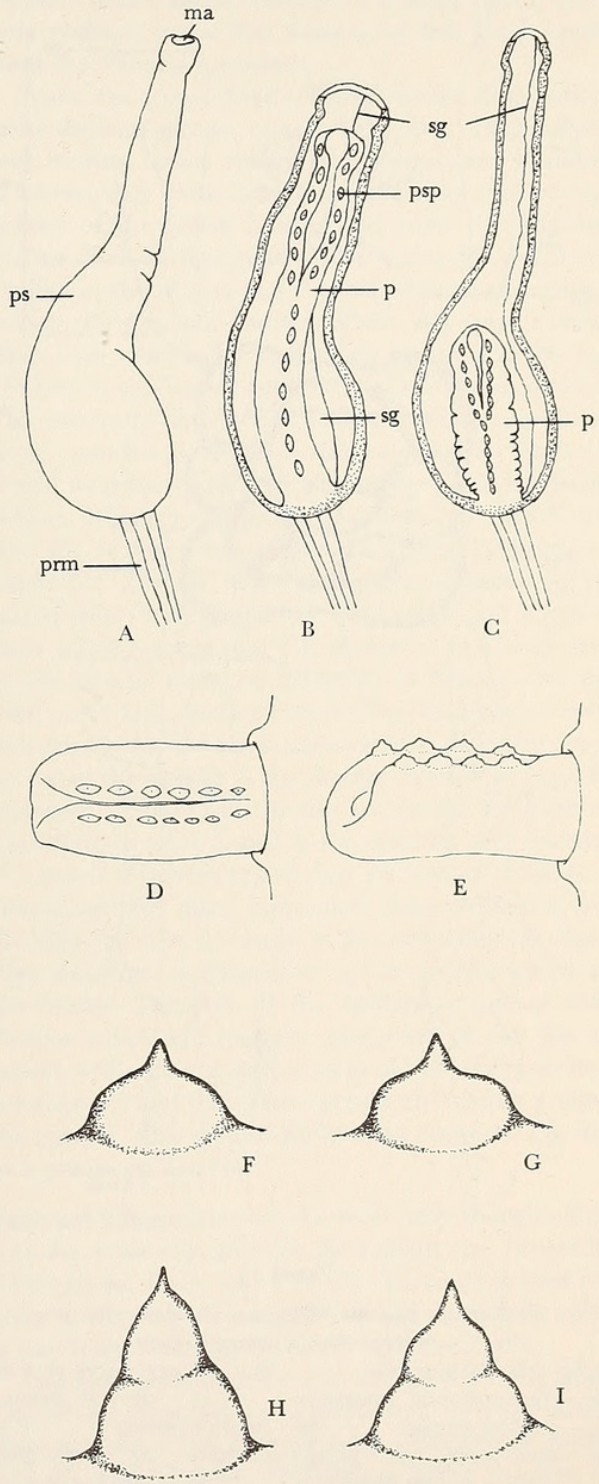
DISCUSSION

Generic Discussion: The subfamily Dolabriferinae contains 3 known genera: *Dolabrifera* Gray, 1847, *Petalifera* Gray, 1847, and *Phyllaplysia* Fischer, 1872. The subfamily is distinguished from other anaspideans by the small, flattened, rounded to spatuliform shell without a strongly curved apex. Often the shell is totally absent. Also in dolabriferans, the parapodia are greatly reduced and as Beeman (1968: 94) describes: "parapodia separated anteriorly by genital groove, broadly joined poste-

(adjacent column →)

Figure 13

Phyllaplysia padinae Williams & Gosliner, spec. nov.
Male reproductive structures
A: dorsal view of male reproductive system; B, C: dorsal half of penial sheath removed; B: penis partially extended; C: penis contracted; D: dorsal view of tip of penis; E: left lateral view of tip of penis; F to I: variation in penial spines
ma – male aperture (male gonopore) p – penis
prm – penial retractor muscle ps – penial sheath
psp – penial spine sg – seminal groove



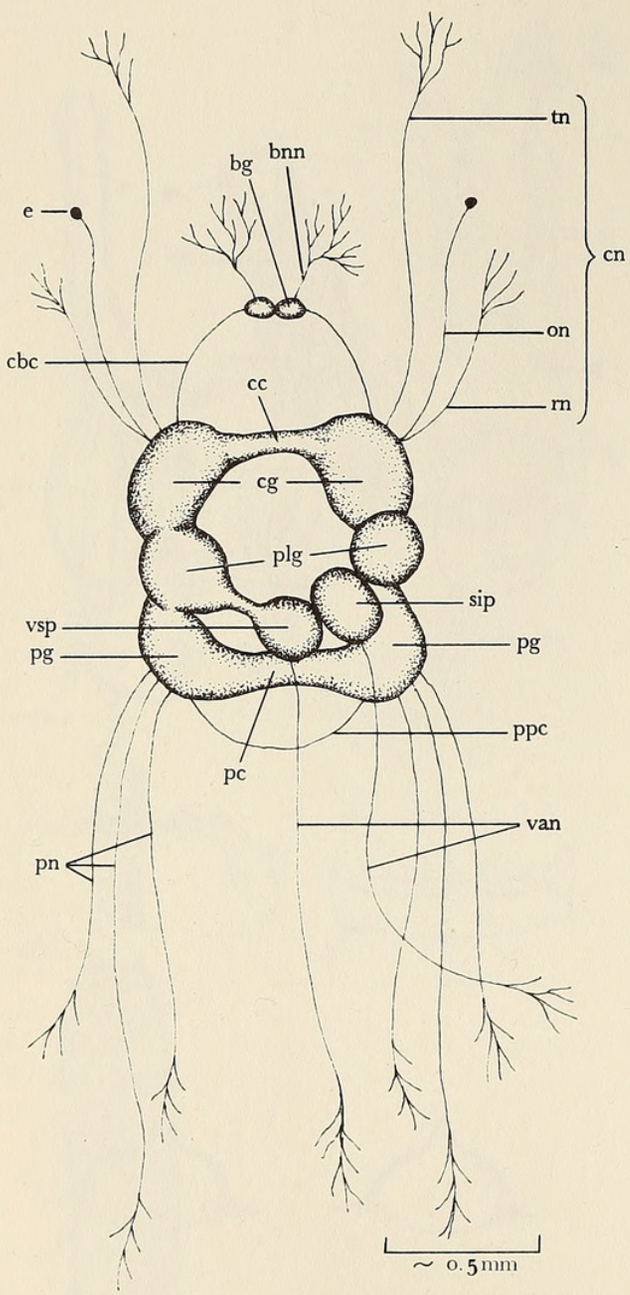


Figure 14

Phyllaplysia ***padinae*** Williams & Gosliner, spec. nov.
Ventral view of nervous system
bg – buccal ganglion bnn – buccal nerve network
cbc – cerebro-buccal connective cc – cerebral commissure
cg – cerebral ganglia cn – cephalic nerves e – eye
on – optic nerve pc – pedal commissure pg – pedal ganglion
plg – pleural ganglia pn – pedal nerves
ppc – parapedal commissure rn – rhinophoral nerve
sip – supraintestinal-parietal ganglion tn – tentacular nerve
van – viscero-abdominal nerves
vsp – visceral-subintestinal-parietl ganglion

riorly, small, not freely motile, often asymmetrical and displaced to the right." The subfamily Dolabriferinae can be distinguished readily from the subfamily Aplysiinae by the greatly shortened visceral loop in the nervous system. As a general rule, anaspideans or other opisthobranchs with well developed motile parapodia have greatly extended visceral loops with posterior ganglia separated from the central nervous system. The regionalization of nervous tissue in this manner consequently allows for decentralized control and greater flexibility in a given area of the body. In this case the nervous control for the extremely well developed, highly motile parapodia in the genus *Aplysia* are directed by a posteriorly located nervous tissue concentration composed of 2 ganglia represented by fusions between the left parietal, subintestinal, and visceral ganglia on the left and the right parietal and supraintestinal ganglia on the right (Figure 15A). In dolabriferans, such as *Phyllaplysia,* the visceral loop has virtually disappeared and the 2 posterior ganglia have migrated to the central nervous system where they are present between the pleural ganglia adjacent to the pedal commissure (Figure 15B). The effect of this migration can be seen externally by the greatly reduced non-motile parapodia.

The distinctions between the 3 dolabriferan genera have been shrouded in confusion in much of the literature. The genus *Dolabrifera* can be separated easily from the others by the presence of a slender elongate shell with terminal knobbed spire and greatly broadened posterior $\frac{1}{3}$ of the body (Beeman, 1968:94). The species *Dolabrifera dolabrifera* (Rang, 1828) is known virtually worldwide from the tropics and has recently been recorded by Bertsch (1970: 110) from Las Cruces Bay, Baja California, in the Gulf of California, and from the Galápagos Islands by Sphon & Mulliner (1972: 149).

Distinctions between the other 2 dolabriferan genera, *Phyllaplysia* and *Petalifera,* are representative of the confusion within the Dolabriferinae. Hyman (1967: 607) states that in *Petalifera* the shell is present and is entirely wanting in *Phyllaplysia.* However, several established species of *Phyllaplysia* are known to possess shells. Marcus (1955: 55) illustrates the shell of *Phyllaplysia engeli* (fig. 4 of that work). Beeman (1968: plt. 11, fig. 2) shows a photograph of the secondary shell of *Ph. taylori.* The shell of *Ph. padinae* is diagrammatically represented in Figure 10. Beeman (*op. cit.*: 94) states that a shell has also been reported by Bergh (1905) for *Ph. inornata* Bergh, 1905. Because of these citations the mere presence or absence of a shell cannot be used as a taxonomically valid factor in differentiating between *Petalifera* and *Phyllaplysia.* Further confusion has also been added in regard to radular characteristics. In the diagnosis of the

genus *Phyllaplysia* P. Fischer (1872: 296) describes the radular teeth as tricuspid ("*dentes linguales tricuspidati, obtusi, non aculeati*"). Thiele (1931: 395 - 399) describes the rachidian teeth of the genus *Petalifera* to be 5-cusped (" ..., Schneide mit 5 Zähnen, ...") and *Phyllaplysia* to be tricuspid ("..., mit dreizackiger Schneide, ...). This would seem to be an easy way to distinguish the 2 genera, except for the fact that *Ph. paulini* Mazzarelli, 1895, *Ph. viridis* (Bergh, 1905), *Ph. varicolor* (Bergh, 1905), and *Ph. taylori* Dall, 1900 all have 5 cusps on the rachidian teeth (and sometimes 7 in *Ph. viridis*). Because of these exceptions the number of cusps on the rachidian teeth also cannot be used as a taxonomic criterion to distinguish the 2 genera.

There are valid characters, however, which are important in distinguishing between the genera *Petalifera* and *Phyllaplysia*. These are concerned with shell structure and foot characteristics. Baba (1959) recognizes only 4 species of *Petalifera*. These are *Pe. petalifera* (Rang, 1828), from the Atlantic and the Mediterranean, *Pe. albomaculata* (Ferran, 1905) of the Indian Ocean, *Pe. punctulata* (Tapparone-Canefri, 1874) from Japan, and *Pe. ramosa* Baba, 1959, from Japan and Florida. All the above listed species of *Petalifera* possess thin shells with terminal apices at one end and crescent-shaped concentric rings emanating outward from the apex. In all species of *Phyllaplysia* possessing a shell the apex is in the middle of the shell, with concentric circles surrounding the apex and extending out toward the margins of the shell (see Figures 15C to 15E for comparison). This basic difference in shell structure seems to be a valid criterion for the taxonomic distinction between the 2 genera.

Also to be considered is the attachment of the anterior region of the foot with the body margin. Marcus (1957: 53) in describing *Phyllaplysia engeli* states: "the anterior border of the foot is occasionally bilabiate. Also, in these cases, it is connected with the lateral margins of the body, so that the difference against *Petalifera* with free anterior border of the foot (Engel, 1936, p. 48; Engel and Hummelinck, 1936, p. 48) continues to be valid." In individuals of *Ph. taylori* and *Ph. **padinae*** observed by us, the anterior margin of the foot and the body margin are attached throughout.

Ecology and Distribution: Of the 12 species of *Phyllaplysia*, only 2 other than *Ph. **padinae*** are known from the coasts of North and South America. *Phyllaplysia engeli* is found from the coast of Florida, throughout the Caribbean, to the northern sector of the State of Saõ Paulo, Brazil. *Phyllaplysia taylori* occurs along the Pacific coast of North America from Vancouver Island, British Columbia, to San Diego, California. No species of *Phyllaplysia* appears to have a worldwide, hemispherical or circumtropical distribution and apparently none occurs on more than a single coastline of a single ocean. *Phyllaplysia **padinae*** is the first member of this genus recorded from the Panamic province.

While the genus *Phyllaplysia* includes distributionally quite disjunct species, certain facts about their substrates and feeding habits remain fairly constant. *Phyllaplysia* is known only from 2 habitats, crawling on the marine grasses of the genus *Zostera* and from the phaeophyte *Padina*. Both of these genera have worldwide distributions, *Padina* in the tropics and *Zostera* in the more temperate waters. *Phyllaplysia **padinae*** is the only species recorded from both substrates. *Phyllaplysia taylori* and *Ph. lafonti* are known on *Zostera* and *Ph. engeli* is known on *Padina*. The substrates on which the other species occur have not been recorded. While the substrate is well known, the actual food source for members of the genus has been the subject of much confusion. MacFarland (1966) stated that *Ph. taylori* feeds on bryozoan colonies found on the blades of *Zostera marina* Linnaeus. Fischer (1870) stated that *Ph. lafonti* feeds on *Zostera* and algae. Beeman (1968) noted that *Ph. taylori* in fact feeds on epiphytic diatoms found on the blades of *Zostera*. Our examinations of fecal matter from central Californian individuals of *Ph. taylori* have revealed that the primary food source of this species is the diatom *Isthmia nervosa* Kütz. Marcus (1957) adds to this knowledge by mentioning that diatoms were found in the stomach and intestine of *Ph. engeli*. Fischer's report that *Ph. lafonti* feeds on *Zostera* is perhaps more incomplete than erroneous. In *Ph. **padinae*** the first cell layer of the polystromatic alga *Padina durvillaei* is scraped off as the animal grazes along the blades. The bulk of the epidermal surface cells of *Padina* which are ingested pass through the gut undigested, while the contents of most of the epiphytic diatoms are digested and their tests egested after being ground by the gizzard. This is most likely what occurs in *Ph. lafonti* as it grazes on *Zostera*.

External Characteristics: General body shape and structure are relatively uniform throughout the 12 species of *Phyllaplysia*. Body length of the described species is also quite uniform; most are under 50 mm in length; only *Ph. taylori* is known to exceed this length materially.

Although general shape and size are basically uniform throughout the genus, color patterns do vary considerably. However, most species have been described as having a greenish ground color. *Phyllaplysia plana* is green decorated with yellow and pink spots; *Ph. engeli* is often rusty brown with a greenish hue and sometimes with pinkish mottling; *Ph. taylori* is described by Beeman (1968: 99)

as having a bright green ground color with distinct dark striping; *Ph. ornata* is dark green with yellow spots, while *Ph. paulini* is light green with white longitudinal lines; *Ph. lafonti* is green with white and grey spots surrounded by violet. *Phyllaplysia* ***padinae*** is olive green with random white spots, and *Ph. viridis* is green throughout with branched dorsal processes; lastly, *Ph. varicolor* is greyish to reddish brown with white dots.

Digestive System: The digestive system of most members of the genus *Phyllaplysia* is uniform in structure and shape. It consists of the buccal area, an esophagus, 2 salivary glands, a gizzard with an anterior and posterior portion, a stomach, a large digestive gland, an intestinal tract and an anus at the opening of the pallial cavity. The radula and jaws are of great taxonomic importance and will be considered first.

The jaws in all species of *Phyllaplysia,* where described, have many hook-shaped elements. In *Ph. engeli* these elements are curved with little or no recurving at the apices. In *Ph.* ***padinae*** the apices of the rodlets show considerably more recurving than in *Ph. engeli.* The number of elements of the jaw is not readily ascertainable, and it is extremely difficult to establish differences between species.

The numbers of radular teeth and cusps are probably the most readily quantifiable characters of most mollusks. In *Phyllaplysia* the radula is extremely variable on the interspecific level, and thus is significant in the determination of the taxonomy of the genus. *Phyllaplysia* may have a rachidian plate with either 3, 5 or 7 denticles. *Phyllaplysia* ***padinae*** has 3 denticles on its rachidian plate; only *Ph. engeli, Ph. lafonti,* and *Ph. depressa* share this particular characteristic (compare Figures 15K to 15M). Engel (1936) considers *Ph. depressa* to be identical with *Ph. lafonti,* but does not provide a formal synonymy.

The buccal mass in *Phyllaplysia* ***padinae*** is simply ovoid in shape. Most other species of the genus share this trait. In *Ph. engeli* the buccal mass is ovoid at the anterior end, while the posterior $\frac{2}{3}$ of the mass is decidedly rectangular in shape.

The gizzard teeth in *Phyllaplysia* ***padinae*** are cornucopiate in shape. In *Ph. engeli* these teeth are described as being pyramidal in shape. The teeth in *Ph. engeli* are blunt, stout structures which lack the obvious curvature of those in *Ph.* ***padinae*** (compare Figures 15I and 15J).

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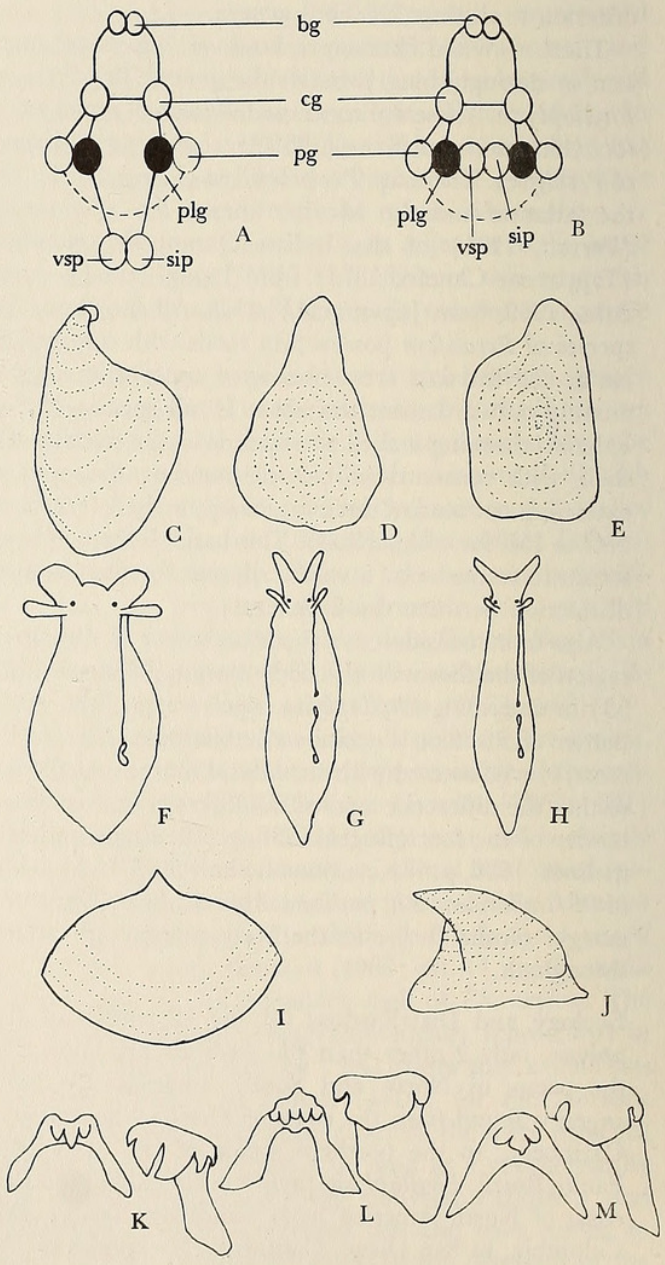

Figure 15

Comparative anatomical diagrams

A: schematic diagram of the nervous system in the Aplysiinae; B: schematic diagram of the nervous system as seen in the Dolabriferinae; C: shell of *Petalifera ramosa* (after Marcus & Marcus, 1967); D: shell of *Phyllaplysia engeli* (after Marcus & Marcus, 1957); E: shell of *Phyllaplysia* ***padinae***; F: body outline of *Phyllaplysia engeli*; G: body outline of *Phyllaplysia taylori*; H: body outline of *Phyllaplysia* ***padinae***; I: gizzard tooth of *Phyllaplysia engeli*; J: gizzard tooth of *Phyllaplysia* ***padinae***; K: rachidian and first lateral tooth of *Phyllaplysia engeli*; L: same teeth from radula of *Phyllaplysia taylori*; M: same teeth from radula of *Phyllaplysia* ***padinae***

bg – buccal ganglia cg – cerebral ganglia pg – pedal ganglion
plg – pleural ganglia sip – supraintestinal-parietal ganglion
vsp – visceral-subintestinal-parietal ganglion

The digestive gland is the largest organ in the body of *Phyllaplysia* and comprises a substantial portion of the posterior portion of the body. In the genus the gland takes the shape of the body itself. In *Ph. **padinae*** the body is fairly slender and elongate, hence the digestive gland is long and slender; in *Ph. engeli* the body is much stouter and the digestive gland also assumes that form (Figures 15F to 15H).

Reproductive System: The reproductive system of *Phyllaplysia* provides a good basis for taxonomic distinction. Various differentiable aspects of the reproductive organs will be discussed.

Most obvious externally is the common genital aperture. Its position is variable between species and is very valuable in taxonomic determination. In *Phyllaplysia lafonti* the aperture is within the parapodial slit, while in *Ph. engeli* it is outside the parapodial cavity, immediately adjacent to the anterior border of the slit. In both *Ph. taylori* and *Ph. **padinae*** the genital opening is approximately $\frac{1}{3}$ of the way between the anterior end of the parapodial slit and the head, considerably anterior to the positions of either of the species mentioned above.

Internally, the second largest organ is the gonad or ovotestis. Beeman (1970) states that whether this organ is lobate or non-lobate depends largely on the state of preservation or degree of dissection. With this we would agree; however, the degree to which this occurs is variable. In *Phyllaplysia engeli* about a dozen follicles occur which are completely distinct from each other. In *Ph. **padinae*** and *Ph. taylori* the ovotestis appears as a solid mass and even in its dissected state the lobes are by no means completely distinct from each other. In *Ph. engeli* the ovotestis mass is short, while in both *Ph. **padinae*** and *Ph. taylori* the mass is a very dense, elongate structure.

In *Phyllaplysia **padinae**,* as well as in *Ph. taylori,* the ampullar region is long and consists of many coiling convolutions. In contrast is the ampulla in *Ph. engeli,* where this structure is very short and shows only a minute amount of coiling.

In *Phyllaplysia **padinae*** the bursa copulatrix opens directly into the common atrium via an elongate tube. This is in contrast wtih both *Ph. engeli* and *Ph. taylori*; in both of these species the bursa empties into the common genital duct rather than into the atrium. The unusual coiling of the genital duct around the tube of the bursa copulatrix also appears to be unique to *Ph. **padinae*** (Figure 12).

The penis in most species of *Phyllaplysia* varies substantially. Marcus (1955 and 1961) adds some confusion to the situation. In his 1955 paper he states quite correctly that *Ph. plana* lacks spines on the penis itself. In 1961 (p. 12) he states: "A smooth penis does not seem to occur in *Phyllaplysia.*", without making any further reference to *Ph. plana.* Apparently, *Ph. plana* is the only species of described *Phyllaplysia* that lacks spines on the penis. The penis of *Ph. **padinae*** is unique in its structure in that it is cleft at the tip. This structure has not been recorded previously for *Phyllaplysia* (Figure 13B).

Nervous System: Significant changes have taken place in the nervous system of *Phyllaplysia* which distinguish it from the idealized primitive opisthobranch proposed by Guiart (1901) (see also Bullock & Horridge, 1965). In *Ph. **padinae*** the nervous system is extremely compact, with all the ganglia contained in the nerve ring surrounding the esophagus. The visceral loop has been shortened (as discussed above under generic discussion), and important ganglionic fusions have taken place, thus concentrating nervous tissue and assimilating it in the central nervous system. On the left side, the visceral, subintestinal, and left parietal ganglia have fused. This has resulted in one ganglion, which has become situated on the nerve ring to the inside of the pleural ganglion. On the right side, the supraintestinal and right parietal ganglia have fused; this also has resulted in one ganglion which has become situated to the inside of the right pleural ganglion. The representative 2 ganglia of these fusions of formerly 5 ganglia are situated adjacent to one another on the inside ventral portion of the nerve ring (Figure 14).

In *Phyllaplysia **padinae*** the cerebral commissure length is about equal to the diameter of one ganglion of the cerebral ganglia. In *Ph. engeli* the commissure is much smaller than the diameter of a single ganglion. The 2 ganglia making up the cerebral ganglia are therefore in very close proximity to each other, almost touching, whereas in *Ph. **padinae*** they are separated to a considerable degree.

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