

A Review of the Genus *Triopha*

(Mollusca : Nudibranchia)

BY

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(3 Plates; 10 Text figures)

INTRODUCTION

SERIOUS TAXONOMIC DIFFICULTIES have long confused our understanding of the genus *Triopha* Bergh, 1880. Although 8 species of *Triopha* have been described from the Californian Pacific coast, only 3 – *T. carpenteri* (Stearns, 1873), *T. maculata* MacFarland, 1905, and *T. grandis* MacFarland, 1905 – appear with any degree of consistency in the literature and in extant collections. The remaining 5 nominal species have remained either uncollected, unrecognized, or ignored. This study seeks to clarify the specific taxonomic problems among the known species of *Triopha*.

The material available in the following museums was examined: California Academy of Sciences, Department of Invertebrate Zoology, San Francisco (CASIZ); Los Angeles County Museum of Natural History (LACM); San Diego Natural History Museum (SDNHM); Santa Barbara Museum of Natural History (SBMNH); United States National Museum, Washington, D.C. (USNM). Material from several smaller collections was also examined, in addition to many live specimens in their original habitat, or in laboratory aquaria, or both.

A total of 439 specimens of *Triopha* was studied. These specimens had been identified as follows: 205 specimens of *T. carpenteri*; 126 *T. maculata*; 43 *T. grandis*; 5 *T. aurantiaca*; and 58 simply *Triopha* sp. In the course of this study many specimens were totally or partly dissected; in a selected few cases histological studies were carried out. A total of 173 radulae was extracted and examined. Notes, working papers, sketches, drawings, photographs, mounted slides, and other materials pertaining to this work have been deposited for future reference with CASIZ. A few mounted radulae have been deposited at LACM, SBMNH, and SDNHM.

Analysis of the data from these specimens resulted in the recognition of only 2 species of *Triopha* in the North Pacific: *T. catalinae* (Cooper, 1863), and *T. maculata* MacFarland, 1905.

SYSTEMATIC ACCOUNT

NUDIBRANCHIA

Doridoidea

Phanerobranchia

POLYCERATACEA

POLYCERATIDAE

Triophinae

Triopha Bergh, 1880

History and Description: BERGH (1880) defined the genus *Triopha* (which he placed within the family Polyceratidae) as: "Body shaped like in *Triopa* [Johnston, 1838] with a similar frontal veil; the appendages along the dorsal ridge are mostly nodose, although sometimes slightly ramose. Tentacles are compressed and cup-shaped (auriform); rhinophores retractile and perfoliated. Gills five-leaved, tri-pinnate. Jaws made of minute rods. Radula with 4 spurious rachidian teeth, 3-4 pleural teeth (with winged body and flattened hook), 10-11 external

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teeth. Prostate?" The description of the type species (*T. modesta*) was based on a single specimen collected by Dall at Yukon Harbor (Shumagin), Alaska, August, 1874. Bergh described *Triopha modesta*, although admitting that "this species may perhaps be the *Triopha carpenteri* of Stearns."

BERGH (1894) redescribed the genus *Triopha*, adding only: "Prostate is large. Penis is armed." He also redescribed *T. modesta* (this time from a preserved 5 cm long specimen collected near Unimak Island, Alaska, June, 1890, at 77m) and relegated the senior *T. carpenteri* (Stearns, 1873) to synonymy.

MACFARLAND (1905) introduced 2 new species of *Triopha* from Monterey Bay, California: *T. maculata* and *T. grandis*. He added to the description of *T. carpenteri* and, on the basis of the structure of the radula, arrived at the conclusion that it was a species "distinct from *T. modesta* Bergh."

COCKERELL & ELIOT (1905) described a single specimen of an orange-colored *Triopha* species from San Pedro, California, which COCKERELL (1908) later named *Triopha aurantiaca*.

COCKERELL (1915) brought *Triopha catalinae* Cooper, 1863, into the genus *Triopha*. He described *Triopha scrippsiana* from La Jolla, California, acknowledging it to be similar to, but distinct from *T. carpenteri*, a distinctness "confirmed by the radula ... (of) 58 rows ... (and) 16-22-2-2-22-16 (teeth formula) ..." He further attempted to differentiate the alleged 6 Californian species: *T. catalinae*, *T. carpenteri*, *T. maculata*, *T. grandis*, *T. aurantiaca*, and *T. scrippsiana*.

O'DONOGHUE (1921) described *Triopha elioti*, distinguishing it from *T. carpenteri* because of color, "white, not yellow," and the lesser number of teeth in the radula, "22 as against 33." In a later work (O'DONOGHUE, 1922), he suppressed *T. elioti* as a junior synonym of *T. aurantiaca*.

O'DONOGHUE (1926) designated *Triopha carpenteri* as type species for *Triopha* and recognized 7 species from the California coast: *T. aurantiaca*, *T. carpenteri*, *T. catalinae*, *T. grandis*, *T. maculata*, *T. modesta*, and *T. scrippsiana*.

RISBEC (1928) synonymized *Triopha* Bergh, 1880, with *Triopha* Johnston, 1838, and *Plocamopherus* Alder & Han-

cock, 1866, under *Plocamopherus* Rüppell & Leuckart, 1828, finding it "impossible to distinguish the three genera." The synonymization has found no acceptance among other workers.

THIELE (1931) placed the genus *Triopha* together with 16 others in the subfamily Polycerinae, family Polyceridae, with *T. modesta* as type species.

ODHNER (1941) brought together the genus *Triopha* with "all of those genera which bear ramose or compound processes, like *Plocamopherus*, *Caloplocamus* ..., *Kalina*" into a new family, Triophidae.

BABA (1957) reported *Triopha carpenteri* in Japan.

STEINBERG (1961), impressed by "the absence of specimens from southern California which were clearly referable to MacFarland's *Triopha maculata*," suggested that the *Triopha* species, so abundant in intertidal waters in southern California, might be a species distinct from the *T. maculata* found in northern (Monterey Bay) waters.

TAYLOR & SOHL (1962), in an outline of gastropod classification, preserved Odhner's (1941) arrangement, and placed the family Triophidae (together with the families Notodorididae, Polyceridae, and Gymnodorididae) in the superfamily Nonsuctoria of the infraorder Phanerobranchia.

MACFARLAND (1966) recognized *Triopha carpenteri*, *T. maculata*, *T. grandis*, *T. modesta*, and *T. elioti* (under which he synonymized *T. aurantiaca*).

BURN (1967) included the genus *Triopha* Bergh, 1880 (together with *Kaloplocamus* Bergh, 1880, *Plocamopherus* Rüppell & Leuckart, 1828, and *Joubiniopsis* Risbec, 1928) in Triophinae s. s., in itself a part of the subfamily Triophinae in the family Polyceridae (sic).

FRANC (1968) retained *Triopha* in the separate family Triophidae, and defined the genus as: "Dorsum smooth; edge of notum with appendages above all in the front. Radular formula: 10-11-3-4-2-0-2-3-4-10-11; jaws triangular; penis armed ..."

Type Species: *Triopha modesta* Bergh, 1880 [= *Triopha catalinae* (Cooper, 1863)] by M.

Remarks: Except for RISBEC (1928), the genus *Triopha* has been accepted without question. Although the radular characteristics were set too rigidly by BERGH

Explanation of Figures 2, 12

Figure 2: *Triopha catalinae* (specimen no. 430): scanning electron micrographs of half a row of the radula (courtesy of Hans Bertsch) [montage] approximately $\times 100$

Figure 12: *Triopha maculata* (no. 408), scanning electron micrographs of half a row of the radula (courtesy of Hans Bertsch) [montage] approximately $\times 100$

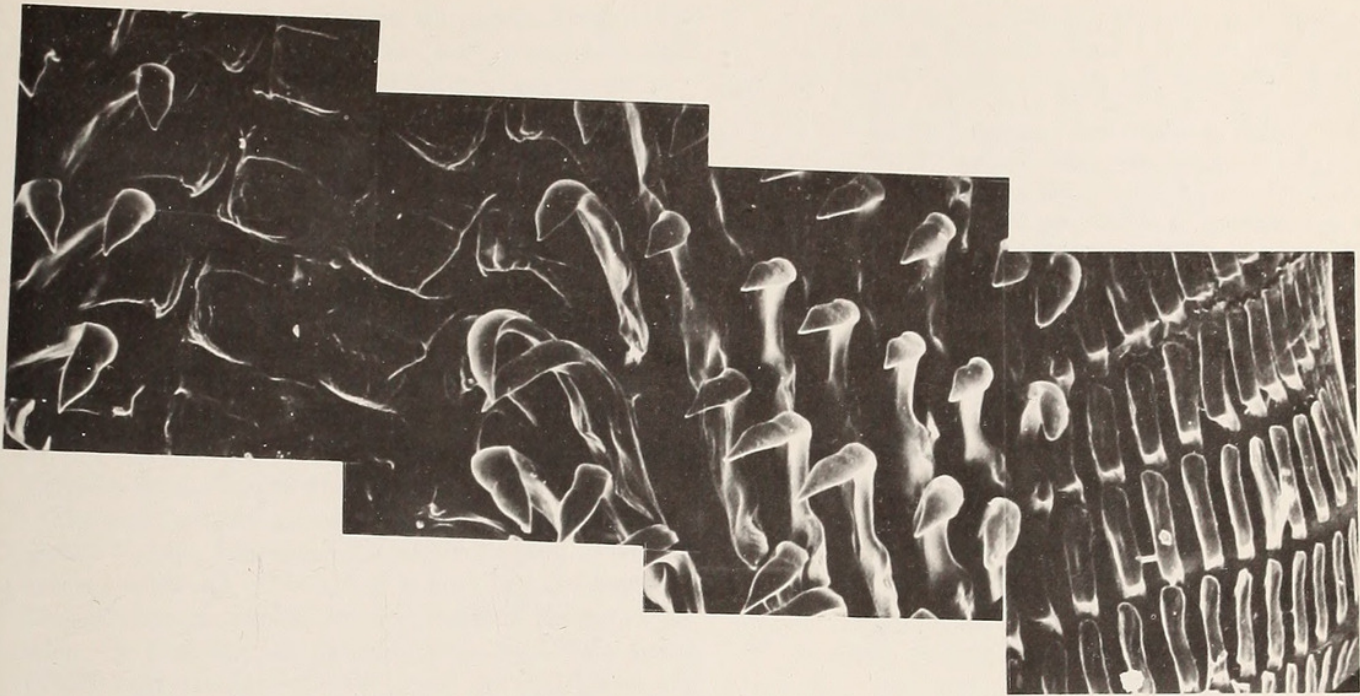


Figure 2

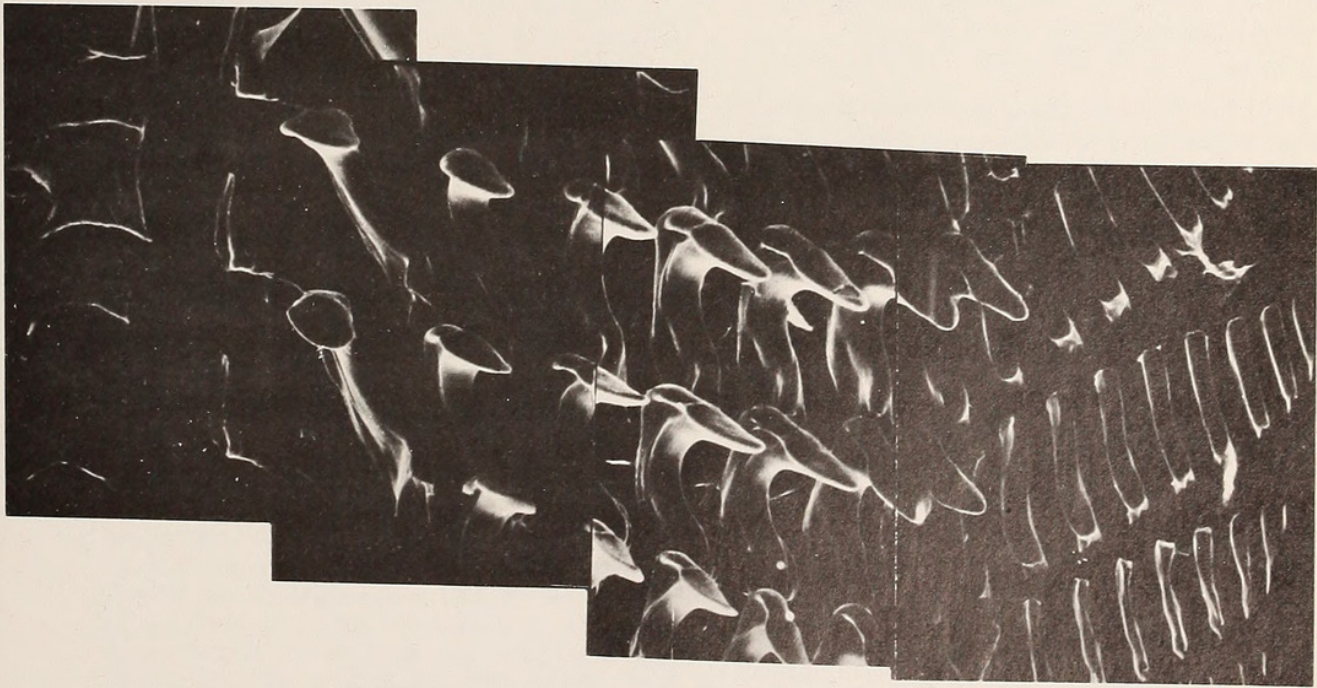


Figure 12

(1880) and subsequent workers, the general external and internal anatomy of *Triopha* has been stated with sufficient clarity to characterize and differentiate the genus.

BERGH (1880) saw *Triopha* as "a link between *Polycera* and *Triopa* on one side, and the Euplocami on the other," and rather close to the genus *Colgae* Bergh, 1880. ODHNER (1941) stressed the taxonomic and phylogenetic importance of the "ramose and compound processes" as a sign of the *Triopha*'s "heritage from ancestors with Dendronotacean features." The systematic importance of frontal and lateral ramose processes in Triophidae was also emphasized by PRUVOT-FOL (1954: 323 - 327), who, although making no reference to *Triopha*, instituted the section Caloplocaminae for 4 European genera, *Issena*, *Caloplocamus*, *Plocamopherus*, and *Crimora*.

The status of the genus *Cabrilla* Fewkes, 1889 (type species by M: *Cabrilla occidentalis* Fewkes, 1889) remains unresolved. Although it is tempting to guess that Fewkes' singular finding was a member of the genus *Triopha*, the fact remains, as pointed out by O'DONOGHUE (1926) and STEINBERG (1961) that the description and illustration of *C. occidentalis* as given by FEWKES (1889) do not correspond to any nominal species of *Triopha*.

Distribution: Currently known species of the genus *Triopha* are confined to the cold-temperate north Pacific, above latitude 30° N, along the coasts of California, Oregon, Washington, Canada, the Aleutian Islands, and Japan, intertidally to subtidally (30m).

Triopha catalinae (Cooper, 1863)

(Figures 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, and 16)

Triopha catalinae Cooper, 1863, 3: 59 (unfigured); COOPER, 1870, 5 (6): 56; ABRAHAM, 1877: 230

Triopha catalinae. COCKERELL, 1915: 229; O'DONOGHUE, 1922, 15: 138; 1926, 15 (2): 214; SMITH & GORDON, 1948, 26 (8): 180; STEINBERG, 1961, 4 (2): 60 (as *nomen dubium*); LANCE, 1961, 4 (2): 66; ABBOTT, 1974: 360, no. 4298

Triopa carpenteri Stearns, 1873, 5: 78; fig. 2; ABRAHAM, 1877: 230

Triopha carpenteri. BERGH, 1880: 112 - 117 (reprinted in DALL, 1880, 1 (6): 261 - 266); TRYON, 1883, 2: 376; BERGH, 1894, 25 (10): 184 (as synonym of *T. modesta*); MACFARLAND, 1905, 18: 48 - 49; COCKERELL & ELIOT, 1905, 12 (3): 43; MACFARLAND, 1906, 25: 135 - 137; plt. 19, figs. 51 - 55; plt. 21, figs. 108, 113; plt. 27, figs. 16 - 17; BERRY, 1907, 21 (3): 35; KEEP, 1911: 125; COCKERELL, 1915, 7: 228 - 229; O'DONOGHUE, 1921, 13 (29): 167; 1922, 15: 136 - 138; 1926, 15 (2): 214, 238; 1927, 19: 95 - 97; JOHNSON & SNOOK, 1927: 495, plt. 10, fig. 1 (reprinted 1967); KEEP, 1935: 274; COSTELLO, 1938,

63 (2): 321 - 326, 330, 333, 334; plt. 1, figs. 11, 21; plt. 2, figs. 26, 31, 38; SMITH & GORDON, 1948, 26 (8): 180; ABBOTT, 1954: 304, plt. 16 k; BABA, 1957, 13 (1 - 4): 11, figs. 1, 2 A; MARCUS, 1961, 3 (Suppl. 1): 22 - 23, plt. 4, fig. 71; STEINBERG, 1961, 4 (2): 60; LANCE, 1961, 4 (2): 64; THOMPSON, 1961: 235; RICKETTS & CALVIN, 1962: 35, plt. 6; STEINBERG, 1963, 6 (2): 70; MACFARLAND, 1966: 106 - 109, plt. 19, figs. 3, 4; plt. 29, figs. 4 - 6; plt. 31, figs. 13 - 18; GHISELIN, 1966, 3 (3): 333, 345; STEINBERG in LIGHT, 1967: 266, 269; HURST, 1967, 9 (3): 255 - 257, 261, 270 - 271; plt. 28, figs. 12, 24; SPHON & LANCE, 1968, 36 (3): 81; RICE, 1968: 461; HADERLIE, 1969, 12 (2): tab. 2; ROLLER & LONG, 1969, 11 (4): 428; TURNER, EBERT & GIVEN, 1969: 137 - 138; MCBETH, 1971, 14 (2): 158 - 160; BERTSCH, GOSLINER, WHARTON & WILLIAMS, 1972, 14 (3): 308 - 312; SPHON, 1972a, 15 (2): 156; ABBOTT, 1974: 360, no. 4295; plt. 17; McDONALD, in SMITH & CARLTON (eds.), 1975: 526, 541; plt. 123, fig. 20

Triopha modesta Bergh, 1880: 113 - 117; plt. 14, figs. 17 - 20; plt. 15, figs. 1 - 11 (reprinted 1880a: 261 - 266; plt. 14, figs. 17 - 20; plt. 15, figs. 1 - 11); 1894: 184 - 187; plt. 7, fig. 29; plt. 8, figs. 2 - 12; plt. 9, figs. 1 - 12; MACFARLAND, 1905, 18: 49; COCKERELL & ELIOT, 1905, 12 (3): 43; MACFARLAND, 1906, 25: 137, 141; O'DONOGHUE, 1922, 15: 137 - 138; 1926, 15 (2): 215; THIELE, 1931: 424; MARCUS, 1961, 3 (Suppl. 1): 22 - 23; MACFARLAND, 1966: 115

Triopha scrippsiana Cockerell, 1915, 7: 228 - 229; O'DONOGHUE, 1926, 15: 137 - 138; 1926, 15 (2): 215; MARCUS, 1961, 3 (Suppl. 1): 23; STEINBERG, 1961, 4 (2): 60; LANCE, 1961, 4 (2): 66; ABBOTT, 1974: 360, no. 4300

Triopha elioti O'Donoghue, 1921, 13 (29): 165 - 167; STEINBERG, 1961, 4 (2): 60; 1963, 6 (2): 70; MACFARLAND, 1966: 115; RICE, 1968: 461

Nomenclatural Comments: STEINBERG's (1961) suggestion that *Triopha catalinae* be considered a *nomen dubium* does not conform well with the fact that COOPER's (1863) description is ample and detailed enough to identify the species later described by STEARNS (1873) as *Triopa carpenteri*. Thus, *Triopha catalinae* is the senior synonym of *Triopa carpenteri* and the proper name for the taxon (International Code of Zoological Nomenclature, Article 23, Law of Priority).

BERGH (1894) had synonymized *Triopha carpenteri* with *T. modesta*, and inexplicably suppressed the former in favor of the latter. Despite the absence of any further data, the nominal species *T. modesta* was regarded as valid by several authors (COCKERELL & ELIOT, 1905; O'DONOGHUE, 1922, 1926; MARCUS, 1961; MACFARLAND, 1905, 1906).

This study shows that the alleged differences in the radulae fall well within the range of individual variation for *Triopha catalinae*; with no other anatomical distinction outstanding, these 3 nominal species are regarded as identical. Similar considerations of radula and external

anatomy apply to the synonymization of *T. scrippsiana*.

O'DONOGHUE (1922) had considered *Triopha elioti* a junior synonym of *T. aurantiaca* Cockerell, 1908. However, the original description and geographical considerations indicate it to be a synonym not of *T. aurantiaca* but of *T. catalinae*, which had been suggested already by STEINBERG (1961: for *T. "carpenteri"*).

Type Material: Unavailable. The "four specimens" upon which COOPER (1863) based his description of *Triopha catalinae* were probably lost or never designated. Equally unavailable are Stearns' (1873, *T. "carpenteri"*), Bergh's (1880, *T. "modesta"*), Cockerell's (1915, *T. "scrippsiana"*), and O'Donoghue's (1921, *T. "elioti"*) original specimens.

Type Locality: "Near north end of Catalina Island [Los Angeles County, California]" (COOPER, 1863).

External Anatomy and Individual Variation: The description by STEARNS (1873), enriched by the observations of BERGH (1880, 1894), MACFARLAND (1905, 1906, 1966), and MARCUS (1961) (using the synonymous name, *Triopha carpenteri*) remain the foundation for the present understanding of *T. catalinae*.

The largest specimen I examined alive (Cypress Point, Pacific Grove, California, September, 1971, at 25 m, leg. Ed Gaffaney, with SCUBA) measured 70 mm in length while actively crawling; the largest specimen preserved in alcohol measured 65 mm. MACFARLAND (1966: 108) mentioned preserving a living specimen 84 mm in length. The material examined in this study indicates that large specimens of *Triopha catalinae* are much more likely to have come from offshore stations and deep water than from intertidal and shallow subtidal localities.

Body shape elongate, limaciform, anteriorly rounded, posteriorly pointed. Color generally white with orange markings. The white ground color often has a translucent quality, particularly noticeable in small specimens. Smaller specimens tend to be diffuse pale yellow, and show a sprinkle of ill-defined white specks on the dorsum and sides. Other specimens have a diffuse dark pigmentation, particularly in the dorsum in front of the gills. In the extreme cases, the pigmentation may turn the ground color to a markedly dark gray. These variations in general color are vaguely related to size and age. Certain color characteristics can be related to geographic populations. For instance, in a lot of *Triopha catalinae* collected at Seals Rock State Park, Oregon, all specimens (small) exhibited a solid translucent white color; in a lot collected intertidally at Orcas Island, Washington, all 5 specimens showed a very heavy pigmentation of the dorsum and the sides; 2 specimens collected together in about 20 m, off Cypress Point, Pacific Grove, California, were intensely

yellow, gradually shading to brown in front of the gills and to white towards the sides.

Less variation occurs in the brilliant orange to vermillion markings of *Triopha catalinae*. These markings appear as well defined, more or less circular blotches in the dorsum and sides. The same orange color is present in the tip of the tail, tips of branchiae, clavus of the rhinophores, dorso-lateral papillae, dorsal tubercles, and appendages of the frontal veil. Nevertheless, the amount and hue of the orange markings varied from specimen to specimen.

In preserved material, the orange color tends to disappear rather rapidly, often in a matter of weeks. This, of course, has much to do with the preserving method and agents. However, it was noticed that the (seemingly) same preserving technique "allows" the orange markings to remain sometimes only for a few weeks, other times for several months.

The head is somewhat flattened dorso-ventrally, and oblique in relation to the body axis. Anterior margin extends into a narrow frontal veil, bearing a variable number (7 to 16+) of small processes which are irregularly shaped, often dendritic, and for the most part intensely orange-vermillion. The frontal veil terminates on the side of the head behind the rhinophores where the row of dorso-lateral tuberculated papillae begins.

The dorsum is slightly arched, delimited on the sides by a row of tuberculated papillae. These papillae, usually 5 or 6, but sometimes as many as 8 or 9 per side, are moderately variable in size and thickness. Often they are blunt, rounded or cylindrical, somewhat granulose, colored a bright orange-vermillion. They lie in a row along a line (that sometimes actually forms a small ridge) separating the dorsum from the sides, and extending from the rhinophores to the tail. A set of round, low-profile dorsal tubercles is virtually diagnostic. These tubercles are usually lined up 4 to 6 in a midline series. About mid-dorsum, this linear series forks into 2 parallel rows of similar tubercles that extend onwards to the sides of the branchiae (often further back to the tail). In their distribution along the dorsum, they outline a sort of inverted Y, to which MACFARLAND (1966: 107) has already called attention. Often, but not always, these dorsal tubercles are orange-vermillion.

The skin, besides the usual glands, contained a large number of spicules in the subepidermal connective tissue. The spicules (Figure 1) were of 2 types: 1) small, about 200 μ m long, spindle-shaped, grouped in tufts or rosettes scattered more or less uniformly throughout the dorsum, sides, and tail; and 2) much larger rods, about 400 μ m to 600 μ m in length, often with a nodosity, knob, or small branch at midpoint, grouped in palisades mostly

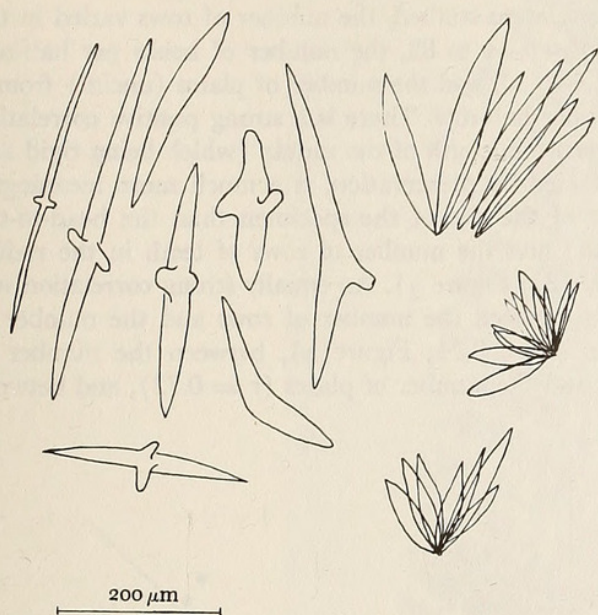


Figure 1

Triopha catalinae

spicules (specimen no. 105) (camera lucida drawing)

along the dorso-lateral ridge to which they seemed to lend support. BERGH (1880: 115) reported the presence of "few and small" spicules in his *Triopha modesta*. Curiously, no other investigator has reported them in this species. Even more curious is that of 10 specimens of *T. catalinae* examined for spicules, only 7 had them as described above. The other 3 specimens (in no other way distinct) had no spicules, a lack which could be related neither to age (size) of the specimen, geographic origin, nor preserving method.

The rhinophores are perfoliated (18 to 35 leaves in the adult); the stalk is cylindrical and well formed, the clavus is curved backwards and upwards. The rhinophores are retractable into thin and smooth rhinophoral sheaths,

The non-retractable branchiae are usually tripinnate, with 5 plumes. Specimens with 4 or 6 plumes are not rare. The plumes are arranged as a pentagonal figure, with the anterior plume in the midline; they surround the centrally located, prominent (often orange-colored) anal papilla. A minute renal pore opens to the right and to the front of the anal papilla.

The tentacles are auriform, tending to appear as if slit along the outer edge.

The foot is uniformly white in color. The anterior margin is rounded and entire, and the sides are nearly

parallel, terminating posteriorly in a somewhat abrupt and blunt point.

The mouth has full plicated lips. The opening is circular, or a vertical slit or an inverted T.

Internal Anatomy: Jaws or mandibular plates are brownish-yellow, nearly triangular, broad above and pointed below. Moderate variations in size and shape are common. Histologically, they are made up of tightly packed hyaline rodlets about 5 μ m in diameter.

The pharynx is conical in shape, relatively large and muscular. Its floor is occupied by the radula which projects posteriorly into the radular sac. In the upper posterior corner there are the openings for the esophagus and the paired pharyngeal glands.

The pharyngeal glands are tubiform, long (as much as 2 or 3 mm in an average sized specimen), and whitish in color. Placed longitudinally between the visceral mass and the foot, they open in the pharynx almost at the same level as the esophagus.

The radula (Figure 2) is broad, deeply grooved and relatively large. The teeth are usually transparent and clear. However, the radular teeth of many specimens, particularly larger (older) ones, were more or less intensely amber colored. The rachidian part of the radula is devoid of teeth; instead, the radular membrane displays at that level some well-defined thickenings (counted as "teeth" by some authors). These thickenings include 1) a roughly quadrangular area located medially (often divided into 2 equal halves by an antero-posterior clearing), and 2) 2 triangular thickenings, symmetrically located on each side of the median thickening. Considerable variation was found in the size, shape, and homogeneity of these median and paramedian thickenings.

The radula of *Triopha catalinae* has been one of the main sources of confusion in previous efforts to understand the concept of the species. The first mention of the radula of *T. catalinae* came from BERGH (1880: 115 to 116) in the description of his *T. "modesta"*: "The total number of rows twenty-one The rhachis rather broad, bearing two quadrangular thickenings of the cuticula ... at the outer side of which there is a somewhat shorter and narrower plate The three succeeding teeth are brownish-yellow, hook-shaped, all nearly of the form and of the same, but outwardly slowly decreasing, size (plt. XV, fig. 6 c, d); the fourth lateral plate ... with a small hook (fig. 7 a) On the lateral parts of the pleurae, ten to eleven external (uncinal) plates ..." MACFARLAND (1905: 48) described the radula of *T. catalinae* (under *T. "carpenteri"*) as composed of 33 rows of teeth, "the rachis broad with four rows of flattened plates (spurious teeth) ...; the pleural teeth yellow, strongly

hooked ... the number varying in different individuals from 9 to 18 ...; uncini ... varying from 9 to 18 in number in different individuals ...," a description left unchanged in his posthumous publication (MacFarland, 1966: 115).

The present investigation disclosed a very different view of the radula of *Triopha catalinae*, with important implications to the study of the radula of nudibranchs in general. The radula of *T. catalinae* was found to vary considerably with the size (age) of the specimen. The radular length varied from 2 to 21 mm in the adult, and it was found to be a direct function of the size of the animal (positive correlation, $r = 0.65$). In the adult, the numbers of radular rows and teeth per row were found

to be also a function of the size of the specimen. Thus, in the specimens studied, the number of rows varied in the adult from 14 to 82, the number of hooks per half-row from 4 to 33, and the number of plates (uncini) from 7 to 28 per half-row. There is a strong positive correlation between the length of the radula (which being rigid and unaffected by preservation, is a much more meaningful index of the size of the specimen than the head-to-tail length) and the number of rows of teeth in the radula ($r = 0.81$; Figure 3). An equally strong correlation was found between the number of rows and the number of hooks ($r = 0.94$; Figure 4), between the number of rows and the number of plates ($r = 0.72$), and between

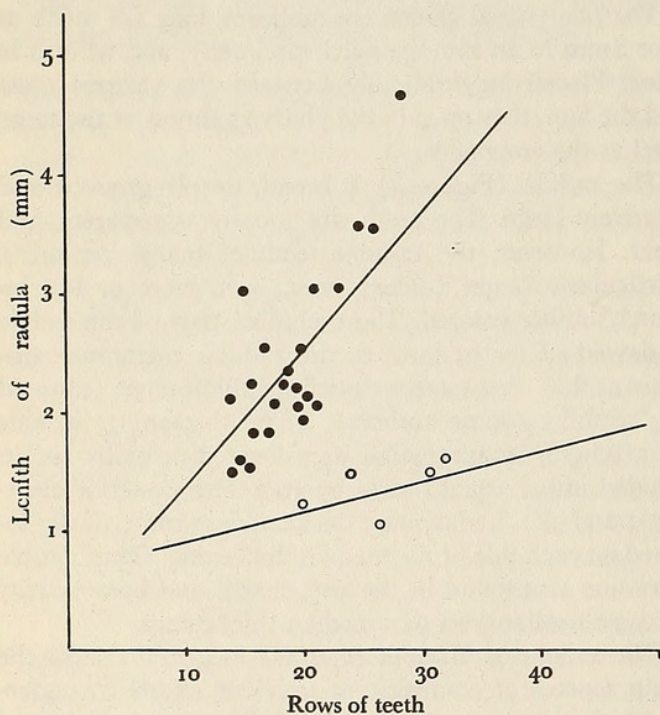


Figure 3

Triopha catalinae

juvenile specimens (*i. e.*, without genital pore); length of radula (in mm) vs. number of rows of teeth. Two populations: ○ "very juvenile" (radula with only one hook per half-row), and ● "less juvenile" (radula with 2 or more hooks per half-row)

$$Y = 0.32 + 0.108 X \quad r = 0.81 \quad p < 0.001$$

$$Y = 0.59 + .027 X$$

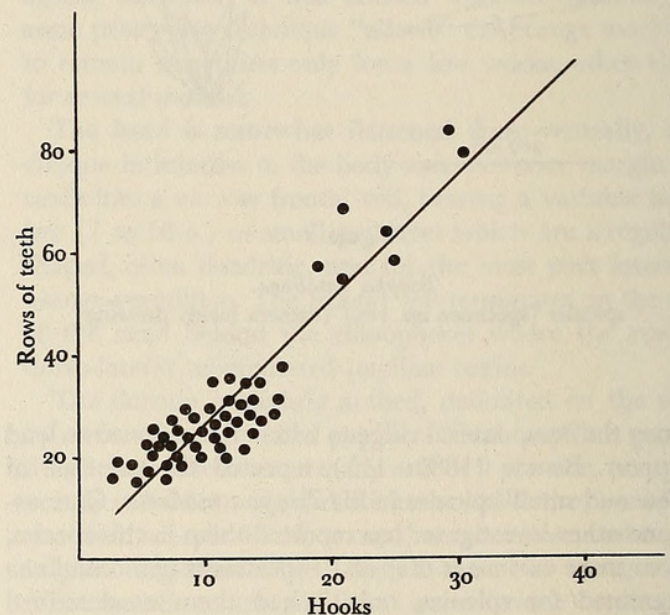


Figure 4

Triopha catalinae

adult specimens: number of rows of teeth in the radula vs. number of hooks per half-row

$$Y = 4.82 + 2.11 X \quad r = 0.94 \quad p < 0.001$$

the number of hooks and the number of plates per row ($r = 0.77$; Figure 5).

Explanation of Figures 6, 7

Figure 6: *Triopha catalinae* (no. 27), radula of very juvenile specimen $\times 40$

Figure 7: *Triopha catalinae* (no. 27), close-up of radula showing paramedian tooth and hook $\times 400$

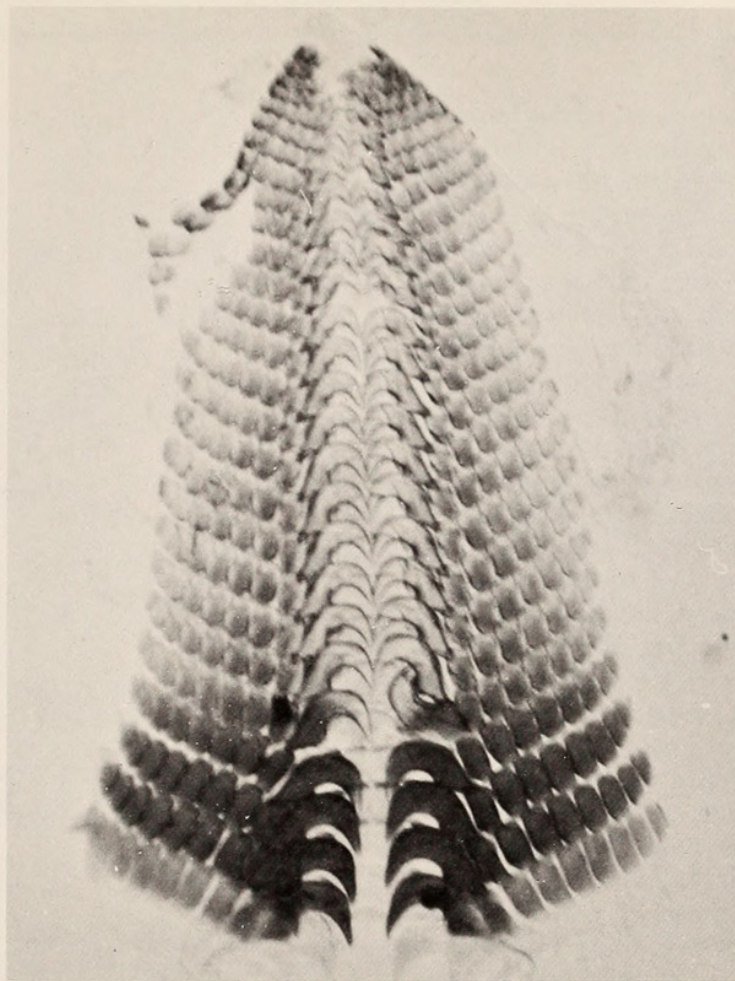


Figure 6



Figure 7

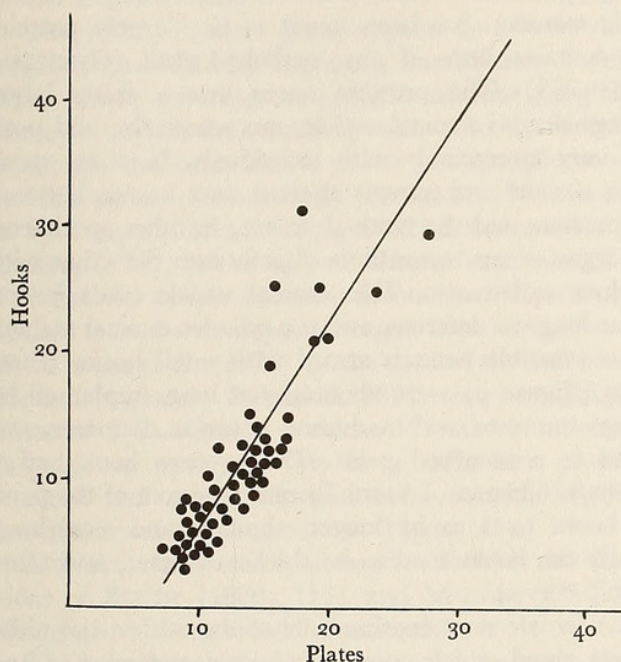


Figure 5

Triopha catalinae

adult specimens: number of hooks vs. number of plates per half-row
 $Y = -10.87 + 1.58 X$ $r = 0.77$ $p < 0.001$

Thus, looking upon these data as a growth series, it becomes apparent that as the animal grows older (larger) the numbers both of rows and teeth per row increase. In *Triopha catalinae*, the merial characteristics of the radula (*i. e.*, size, number of rows, number of teeth) are dependent upon the size (age) of the specimen. What remains constant is not the raw number of these elements (the formula), but the proportions between them. This relationship is also true for the anaspidean *Phyllaplysia taylori* Dall, 1900 (BEEMAN, 1963), and various species of chromodorid and discodorid nudibranchs (BERTSCH, 1976 and personal communication). It is likely to be a valid generalization for a wide number of opisthobranch species (BERTSCH, 1976b).

The problem of the radula of *Triopha catalinae* gets still more complex. The radula of very young specimens (*i. e.*, specimens smaller than 10mm alive, with a radula smaller than 2mm in length) has a much greater number of rows (20 to 33) than the radula of mature individuals; in addition it bears only one hook and 7 to 12 much shorter, squarish plates. In the smallest of these specimens, instead of a triangular paramedian thickening, a

small triangular tooth was present, with a very small cusp directed forwards and inwards (Figures 6 and 7). Indubitably, this paramedian tooth is the precursor of the paramedian triangular thickening of the radular membrane found in the adult radula. MARCUS (1961) has already made this same observation for *T. maculata*, pointing out that the presence of such a paramedian tooth "establishes the origin of the spurious rachidian elements [*i. e.*, the median and paramedian thickening] of the radular membrane by retrograde development of true teeth." In one case (specimen no. 134, SBMNH 23558, *leg.* Tajiguas, Santa Barbara, California, January, 1963, by D. Olsen) this transition from juvenile to adult was seen in the same radula. The specimen in question was the largest (10mm long, preserved) of those "very juveniles" that exhibited paramedian teeth. The radula, also the longest in the group, measured 1.8mm, and it had only 16 rows of teeth (*i. e.*, more like an adult's than a juvenile's). The anterior (oldest) 3 rows had only 1 hook and a paramedian tooth on either side of the quadrangular thickening of the membrane. In subsequent rows the paramedian tooth was progressively less distinct, becoming absent in the posterior (most recent) half of the radula, where it was replaced by the triangular paramedian thickening. Apace with this change, the number of hooks increased from 1 in the anterior rows to 3 in the last row. That such a transition could be observed in a single radula indicates that it must take place at least as rapidly as it takes the whole radula to rejuvenate itself.

In a few prosobranchs and pulmonates, ISARANKURA & RUNHAM (1969) have shown that the rate of secretion of the radula is on the order of 1 to 6 rows per day, and that for a given species the rate was much faster in the young. If these observations are any indication of events in nudibranchs, we may surmise that the juvenile-to-adult transition in radular morphology of *Triopha catalinae* takes place rather rapidly. My attempts to determine the rate of radular replacement in a few adult and juvenile specimens of *T. catalinae* by means of the "cold shock" technique (ISARANKURA & RUNHAM, *op. cit.*) met with no success.

The esophagus leaves the pharynx at its postero-superior corner. It turns to the left (in one specimen it turned to the right first, making a short loop), and enlarges into a stomach. After the stomach, a tubular intestine turns to the right to pass along the space that separates the 2 lobes of the midgut gland where it receives the openings of digestive glands. As a rule, the intestine merges on the lower right side of the animal, curving upward and forward to terminate at the anus, which opens on the anal papilla in the center of the gill branches. The whole di-

gestive tract, from the pharyngo-esophageal juncture onwards, is quite variable in diameter and even in course from specimen to specimen. The midgut gland is voluminous, dark brownish in color, and clearly divided into antero-superior and postero-inferior lobes. Macroscopically, in the specimens examined, the digestive component of the midgut gland could not be told apart from the hermaphroditic gland (ovo-testis) component.

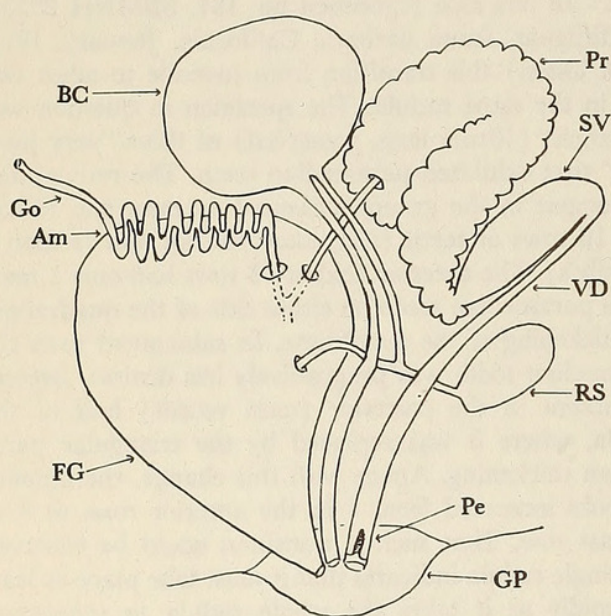


Figure 8

Triopha catalinae

reproductive system (semi-schematic)

- | | | |
|---------------------------|-----------------------|-------------------|
| Am - ampulla | BC - bursa copulatrix | Go - gonoduct |
| FG - female gland mass | GP - genital pore | Pe - penis |
| RS - receptaculum seminis | SV - seminal vesicle | VD - vas deferens |

The reproductive system (Figure 8) is triaulic (SCHMEKEL, 1972), and as described by MARCUS (1961) and MACFARLAND (1966). However, the specimens examined in this study showed greater variability in the relative size of the organs involved than anticipated. From the rather diffuse hermaphroditic gland in the antero-superior lobe of the midgut gland, the gonoduct follows a more or less straight course towards the upper surface of the nidamental gland, where it becomes intensely convoluted in the ampulla. The post-ampullar duct divides

into the male and female ducts. The male duct leads into a large, glandular looking prostate, whose strongly eosinophilic secretion has been found to be "largely protein, and contains little, if any, carbohydrate." (GHISELIN, 1966: 333). The prostate opens into a fairly large, sausage-shaped seminal vesicle, but whose size and position vary appreciably with individuals. In some specimens, a short and narrow efferent duct is seen between the prostate and the seminal vesicle; in other specimens, one organ seems to continue directly into the other with no duct in between. The seminal vesicle leads into a rather long vas deferens, and the cylindro-conical atrium, whose eversible penis is armed with small hooks. These hooks (Figure 9) were about 30 μ m long, implanted by a large round or oval base some 12 μ m in diameter, and ended in a recurved point. The average hook had a midshaft thickness of 5 μ m. Towards the root of the penis the hooks tend to be longer, thinner, and straighter; distally the hooks tend to be thicker, shorter, and more sharply curved.

The female duct continues its course within the nidamental gland which opens, ultimately, posterior to and independent of the vaginal duct. The vagina itself is continued upwards by a relatively long insemination duct which ends in a rather large bursa copulatrix. From the bursa copulatrix (usually quite adherent to the prostate) a thin duct leads to the closed-sac receptaculum seminis, and the female gland mass. This mass, usually large and round, often clearly shows, particularly in the fresh specimen, its 2 component parts, the albumen and the nidamental glands.

The genital pore opens on the right side of the animal, behind and below the right rhinophore. Its size varied with the size of the specimen. It was totally absent in the very small specimens, thus revealing their sexual immaturity. In the smallest specimens examined, neither macroscopic dissection nor microscopical perusal could show the presence of the reproductive system. In a few less juvenile specimens, although the genital pore was still absent, dissection showed a reproductive system minuscule in size but fully formed, with the still undeveloped sexual ducts, vas deferens and insemination ducts, attached to the body wall at the point where the genital pore would later open to the outside.

The cardiovascular system consists of an oval to pyriform heart, about 3 mm in length (for an average sized specimen), located in the posterior part of the dorsum in front of the gills, from which a single median aorta departs in a forward course. The main vessels, only superficially studied, seemed to vary considerably in number and location. In the laboratory, the heart rate of 2 small specimens (10 - 11 mm long while crawling active-

ly) was measured by visual inspection at 72 to 82 contractions per minute.

The juxtaganglionic gland appears as a somewhat irregular, glandular looking mass, immediately under the skin, usually covering the cephalic nervous ganglia and the eyes. Its size varied considerably with the individual. Although the exact nature of the juxtaganglionic gland is still a matter of controversy (SANCHEZ, 1962; SANCHEZ & SABLIER, 1962; MARTOJA, 1965; SCHMEKEL & WEISCHER, 1973), in the case of *Triopha catalinae* (Figure 10) its microscopic structure favors the endocrine-gland rather than the hemopoietic-organ hypothesis. As noted by MILLER *et al.* (1973) in the case of the red abalone, *Haliotis rufescens* Swainson, 1822, the juxtaganglionic tissue of *T. catalinae* is devoid of ductal formations, and is made up mostly of very large cells with prominent nucleoli and acidophilic inclusions, strongly suggesting an endocrinal gland structure (Figure 11).

The nervous system conformed well with the descriptions of BERGH (1880: 114) and MARCUS (1961), although with more individual variation.

The eyes, 2 coal-black dots on top of the antero-lateral aspect of the cerebral ganglia, were often visible in young specimens through the translucent skin.

Behavioral Observations: Little is known about the feeding habits of *Triopha catalinae* except for its appetite for some arborescent ectoprocts. McBETH (1971: 158-160) found through gut analysis of over 100 specimens of *T. catalinae* freshly collected from 25 - 35 m off San Diego, California, that their diet included 3 species of ectoprocts, *Scrupocellaria diegensis* Robertson, 1905, *Crisia serrulata* (Gabb & Horn, 1862) and *Cellaria mandibulata* Hincks, 1882. In this study, the examination of a few live specimens (from 15 - 25 m, off Isla de Todos Santos, Baja California, Mexico) revealed the presence of 3 species of ectoprocts, *Crisia* and *Scrupocellaria* spp. (probably the same as those reported by McBETH, 1971), and *Cellaria mandibulata*.

COSTELLO (1938: 328), from intensive collecting during the years of 1934 - 1936 in the Monterey Peninsula, California, observed that *Triopha catalinae* was to be found in the greatest numbers during the months of July to August. BERTSCH *et al.* (1972) made the same observation in a 5-year period of collecting along the open coast of San Mateo County, California; they witnessed *T. catalinae* crawling on the ectoproct *Membranipora* sp., and on a great diversity of algae, *Corallina*, *Phyllospadix*, *Microdalia*, *Prionitis*, *Hymeneia*, and *Botryoglossum*. Floating behavior has been observed both in the field and in the laboratory (personal observation; also BERTSCH *et al.*, *op. cit.*).

Egg-Laying, Egg Masses, and Veligers: Egg-laying in the laboratory has been found to be most pronounced in July to August, although activity has also been seen in January and February (COSTELLO, 1938). In the laboratory, HURST (1967) observed that egg masses were laid only between April and June. COSTELLO (*op. cit.*) described a period of "restlessness" preceding the laying of eggs in the laboratory.

The egg masses of *Triopha catalinae*, observed in the laboratory, are white, neat counterclockwise-coiled ribbons with the free edge considerably longer than the attached edge. They are of Type A, as described by HURST (1967): "The ribbon is about 1.4 cm wide. Capsules are smooth-walled and may contain 1 or 2 eggs, those with 2 being larger and more oval, some being pointed at one end. Capsules with only 1 egg are more numerous, but in a few egg masses capsules with from 5 to 7 eggs were frequent" (HURST, *op. cit.*: 261; plt. 28, fig. 12). The veligers, also studied by HURST (*op. cit.*, fig. 24; no. 9, table 9) are of Type 1 of THOMPSON (1961: 234 - 235): "Spiral shells normally forming $\frac{3}{4}$ to 1 whorl only." Based on the observation of 10 specimens, HURST (*op. cit.*, table 9) gives the following average measurements for the veliger of *T. catalinae*: 134.5 μ m in length, 89.1 μ m in width, and 97.7 μ m in depth.

Distribution: *Triopha catalinae* has been found in relative abundance along the shores of the North Pacific cold-temperate region, along the coasts of Mexico (Baja California), United States (California, Oregon, Washington, Alaska, and the Aleutian Islands), Canada (British Columbia), and Japan.

The southernmost finding of *Triopha catalinae* was at Isla de Todos Santos (31°48'N; 116°48'W), Baja California Norte, Mexico, in 15 to 25 m of water (7 specimens, September 24, 1973, *leg.* AJF with SCUBA). The northernmost finding was Coghlan Island (58°20'N; 134°42'W), Auke Bay, Alaska, at 8 to 12 m depth (3 specimens, August 4, 1974, *leg.* L. Barr with SCUBA).

Triopha catalinae has been collected at many other in-between stations, including Monaska Bay, Alaska; San Juan Islands, Washington; Catalina Island and Cortez Banks off the southern coast of California. It has also been collected at Amchitka Island in the western Aleutians (Lou Barr, personal communication). In Japan it has been collected at Hirota Bay (39°N; 142°W) on the east coast of Honshu, and at Shirikishinai (41°40'N; 141°10'W) near Hakodate, Hokkaido (BABA, 1957). Detailed sketches of the specimens collected (kindly provided by Dr. Kikutarô Baba) leave no doubt as to their identity.

Most specimens of *Triopha catalinae* examined in this study came from intertidal stations. Many came from kelp beds and coralline algae habitats. The greatest recorded depth was 60m (2 specimens, CASIZ, off San Jose Creek Beach, south of Carmel, California, August 17, 1962, leg. D. Sullivan, with SCUBA).

Triopha maculata MacFarland, 1905

(Figures 12, 13, 14, 15, 17, 18)

Triopha maculata MacFarland, 1905, 18: 49 (unfigured); COCKERELL & ELIOT, 1905, 12 (3): 43; MACFARLAND, 1906, 23: 137-139, 141; plt. 28, fig. 18; BERRY, 1907, 21 (3): 35; KEEP, 1911: 125; COCKERELL, 1915, 7: 229 (key); O'DONOGHUE, 1926, 15 (2): 214-215; JOHNSON & SNOOK, 1927: 495-496; plt. 10, figs. 2, 3 (reprinted 1967); O'DONOGHUE, 1927, 19: 95, 98-99; KEEP, 1935: 274; COSTELLO, 1938: 324, 334, tables 1, 2, 3, 5; SMITH & GORDON, 1948 26 (8): 180; ABBOTT, 1954: 304; plt. 16 f; MARCUS, 1961, 3 (Suppl. 1): 23-24; plt. 4, figs. 72-76; table 1; STEINBERG, 1961, 4 (2): 61; LANCE, 1961, 4 (2): 66; RICKETTS & CALVIN, 1962: 79, fig. 40; FARMER & COLLIER, 1963, 6 (2): 62; STEINBERG, 1963, 6 (2): 70; MACFARLAND, 1966: 109-112; plt. 19, figs. 5, 6; plt. 31, figs. 19-21; FARMER, 1967 9 (3): 341; STEINBERG in LIGHT, 1967: 267-269; SPHON & LANCE, 1968: 36 (3): 81; ROLLER & LONG, 1969, 11 (4): 428; BERTSCH, GOSLINER, WHARTON & WILLIAMS, 1972, 14 (3): 308, tables 1-5; ABBOTT, 1974: 360, no. 4260, plt. 17; McDONALD, in SMITH & CARLTON (eds.) 1975: 526, 541

Triopha grandis MacFarland, 1905, 18: 50 (unfigured); COCKERELL & ELIOT, 1905, 12 (3): 43; MACFARLAND, 1906, 25: 139-141; plt. 19, figs. 60-64; plt. 28, fig. 19; COCKERELL, 1915, 7: 229; O'DONOGHUE, 1922, 15: 137-138; 1926, 15 (2): 214; 1927, 19: 95, 97-98; SMITH & GORDON, 1948, 26 (8): 180; ABBOTT, 1954: 304; plt. 16 b; MARCUS, 1961, 3 (Suppl. 1): 23, table 1; LANCE, 1961, 4 (2): 66; STEINBERG, 1963, 6 (2): 70; MACFARLAND, 1966: 112-118; plt. 19, figs. 1, 2; plt. 31, figs. 22-26; FARMER, 1967, 9 (3): 341; STEINBERG, in LIGHT, 1967: 267, 269; HADERLIE, 1968, 10 (4): tables 2, 3; SPHON & LANCE, 1968, 36 (3): 81; ROLLER & LONG, 1969, 11 (4): 428; HADERLIE, 1969, 12 (2): tables 1, 2; ABBOTT, 1974: 360,

no. 4296; plt. 17; McDONALD, in SMITH & CARLTON (eds.), 1975: 526, 541

Triopha aurantiaca Cockerell, 1908, 22 (9): 42 (unfigured); (= *Triopha* sp. Cockerell & Eliot, 1905, 12 (3): 42-43); COCKERELL, 1915, 7: 229; O'DONOGHUE, 1922, 15: 137-138; 1926, 15 (2): 214; MARCUS, 1961 3 (Suppl. 1): table 1; STEINBERG, 1961, 4 (2): 60-61; LANCE, 1961, 4 (2): 66; ABBOTT, 1974: 360, no. 4299

Triopha sp. SPHON & LANCE, 1968, 36 (3): 81; ROLLER & LONG, 1969, 11 (4): 428; BERTSCH, GOSLINER, WHARTON & WILLIAMS, 1972, 14 (3): 308, tables 2, 4, 5

Nomenclatural Comments: The suppression of *Triopha grandis* as a synonym of *T. maculata* followed naturally from a comparison of the 2 species' descriptions (MACFARLAND, 1905, 1906, and 1966), a side by side examination of the respective holotypes (kindly loaned by US NM), and the present study which included the specimens and material in the MacFarland Collection, CASIZ.

Both names, *Triopha maculata* and *T. grandis*, bear the same publication date. But *T. maculata*, having page priority and greater appropriateness, is adopted here. *Triopha aurantiaca* Cockerell, 1908 first reported as *Triopha* sp. by COCKERELL & ELIOT, 1905), is by description identical to juvenile *T. maculata*. The color, external characters, radula, and locality all attest to this. It has already been synonymized by McDONALD (in SMITH & CARLTON, 1975). From all appearances, it is the same animal which SPHON & LANCE (1968), ROLLER & LONG (1969), and BERTSCH *et al.* (1972) had called simply *Triopha* sp., uncertain whether they were dealing with juveniles of *T. maculata* (as MACFARLAND, 1906 and 1966; and JOHNSON & SNOOK, 1927: 446; plt. 10, fig. 2, had indicated), or a yet to be described new species. Attempts to fully resolve that question (STEINBERG, 1961) were not made until now. With this study, based upon the examination of a fairly large number of specimens varying in size and locality, it was finally possible to visualize a growth series and forms of transition that elucidated and bridged the apparent gap between *Triopha* sp. and *T. maculata*.

Type Material: Holotype of *Triopha maculata* (USNM 181, 276), and holotype of *T. grandis* (USNM 181, 283) are at the United States National Museum, Washington,

Explanation of Figures 9 to 11, 18

Figure 9: *Triopha catalinae* (no. 236), penis hooks, about $\times 400$
Figure 10: *Triopha catalinae* (no. 380), juxtaganglionic gland and ganglionic cell about $\times 40$

Figure 11: *Triopha catalinae* (no. 380), juxtaganglionic gland about $\times 400$

Figure 18: *Triopha maculata* (no. 72), radula of very juvenile specimen approximately $\times 40$

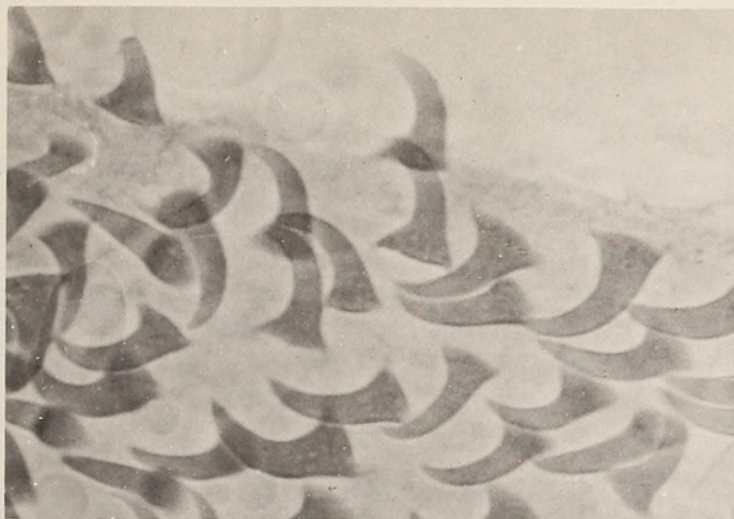


Figure 9

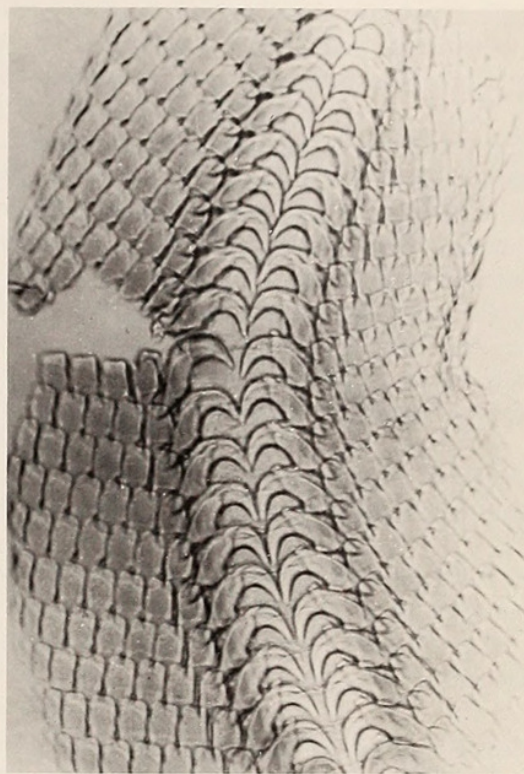


Figure 18

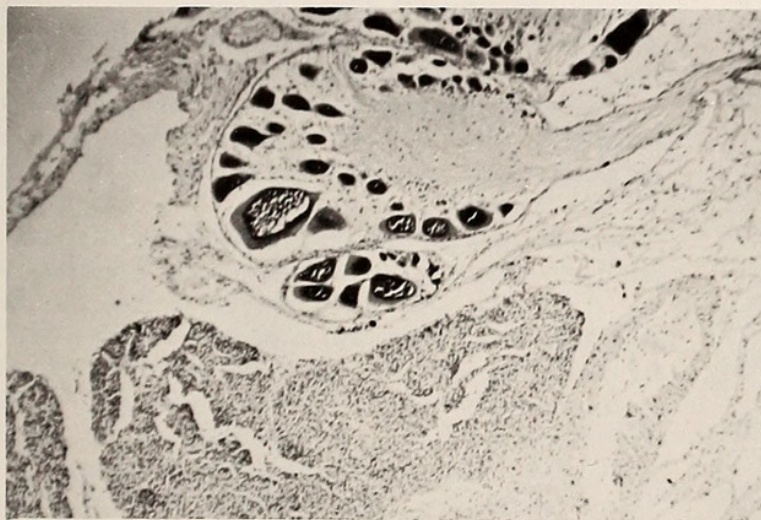


Figure 10

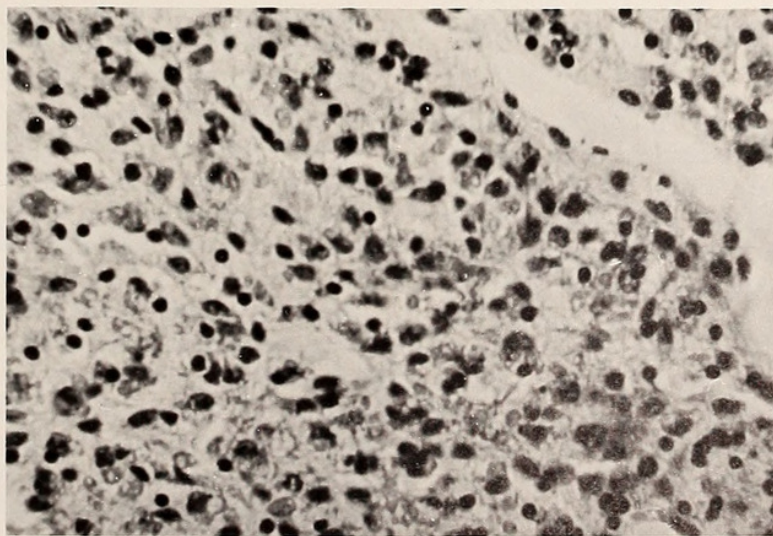


Figure 11



Ferreira, Antonio J. 1977. "A REVIEW OF THE GENUS TRIOPHA MOLLUSCA NUDIBRANCHIA." *The veliger* 19, 387-402.

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